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ECOLOGICAL MONOGRAPHS

VOL. 29

APRIL, 1959

NO. 2

OFFICIAL PUBLICATION OF THE ECOLOGICAL SOCIETY OF AMERICA

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PUBLISHED QUARTERLY BY DUKE UNIVERSITY PRESS
DURHAM, N. C., U. S. A.

ECOLOGICAL MONOGRAPHS

A QUARTERLY JOURNAL
FOR ALL PHASES OF BIOLOGY

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Subscription price: the United States, Canada, and the Pan-American Countries, \$6.00 per year; all other countries—\$6.00 a year additional for postage. Single numbers of the current volume are \$1.75. Back numbers, \$8.00 per volume, \$2.00 per number. Missing numbers will be supplied free when lost in the mails if written notice is received by the Circulation Manager within one month of date of issue. All remittances should be made payable to the Duke University Press, Box 6697, College Station, Durham, N. C.

Agents in Great Britain: The Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1. Prices can be had on application.

Entered as second-class matter December 18, 1930, at the Post Office at Durham, North Carolina, under the Act of Congress of March 3, 1879.

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EVIDENCE OF PHOTOPERIODIC ECOTYPES IN TREES¹

O. VAARTAJA

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INTRODUCTION

Photoperiodism in trees has recently drawn increasing research interest. Short photoperiods or the complementary long dark periods have been found to retard growth and to induce early dormancy in many tree species (Balut 1956, Downs & Borthwick 1956, Wareing 1956, Waxman 1956, Alleweldt 1957, Davidson & Hamner 1957, Olson & Nienstaedt 1957, Nitsch 1957, Robak 1957, Vaartaja 1957a, Zelawski 1957). Decreasing length of day after midsummer appears to be an important factor in initiating the rest period. If this is true, the maximum daylength that retards growth or induces dormancy should be longer for northern than southern trees, and tree species with wide latitudinal range should contain photoperiodically different ecotypes.*

To provide indisputable evidence of photoperiodic ecotypes, photoperiodic treatments of the experiment should be arranged so as to avoid the influence of differences in temperature and in amount of light. This is possible if there is a main light period of high intensity in all treatments and additional light of low intensity in the long day treatments. Another means to avoid the differences in amount of light is to interrupt the dark period with a short period of light in the manner indicated in Table 1.

The suggestion that tree species contain photoperiodically different types was first given by Sylven (1940). He found that progenies of *Populus tremula* L. from Norrbotten in northern Sweden contained more dwarf seedlings than did those from southern Sweden when both were grown at Ekebo in southern Sweden. Crossing of southern and northern trees usually produced an intermediate number of dwarfs. The difference between the normal seedlings and rosetted dwarfs was explained by assuming that the

short days (maximum 20 hrs) of Ekebo inhibited the northern types adapted to long (24 hrs) days. It is difficult to explain, however, why there were dwarfs (0, 0, 0, 3, 7, and 8%) also in some crosses between southern trees.

To explore the hypothesis further Sylven grew *P. tremula* in cold frames, these being uncovered to allow light for the whole day or covered to permit light for 12 hrs a day. Results of this kind of experiment are valuable for exploratory studies, but difficult to interpret in terms of true photoperiodic responses. It is not known how much significance should be attached to the accompanying differences in temperature and in the amount of light.

All seedlings grew well under the long days of latitude 66°. Growth of all seedlings was reduced by covering. This was especially obvious in certain northern progenies, which suggests that northern and southern seedlings were of different ecotypes. When grown under the shorter days in central Sweden (63°), only those seedlings originating north from this latitude appeared inhibited. This is again in accordance with the hypothesis of photoperiodic ecotypes. There were, however, two points in the data that are difficult to explain by this hypothesis alone. One progeny of northern (64°) trees was not much suppressed by covering and the crosses between these trees and certain southern (58°) trees were greatly dwarfed when covered.

Sylven supposed that the *P. tremula* of Sweden consisted of relatively homozygous long day types in the north, of relatively homozygous short day types in the south, and of highly heterozygous types in the central part of Sweden. This two-type hypothesis however can hardly explain the mechanism for the apparently gradual, clinal (Johnsson 1956) differences in *P. tremula* within its wide latitudinal range.

Grehn (1952) found dwarfs in *P. tremula* crosses of parents from Sweden and Germany. All seedlings exhibited rosette appearance but good root formation. He supposed that the dwarfs were a result of the heterozygous types being inhibited by the short days

¹Contribution No. 485, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada, and No. 3, Canada Department of Agriculture Laboratory, Saskatoon, Sask.

*The term "ecotype" is used in this paper in its most general meaning. Gregor (1944) has suggested the term "ecodeme" whenever the ecotypic variation or its significance has not been fully established. "Ecodeme," however, is not well known among many of the readers.

of the test site (54°) in Germany. When seedlings from the same crossings were grown in Sweden (64°) they reached a height three times greater than in Germany. Many (40 to 50%) dwarfs also occurred in crosses between two closely related species from about the same latitude (*P. canescens* (Ait.) Sm. × *P. tremula* and *P. canescens* × *P. nigra* L.). Grehn thought that these dwarfs were not caused by photoperiods. If they were types adapted to northern long days, they should have exhibited good winter resistance, which apparently was not the case.

Data suggesting existence of photoperiodic ecotypes in several American species of *Populus* have been given by Pauley (1950), Pauley & Perry (1954), and Hoffman (1953). Ecotypes from the northern latitudes or from high elevations, when grown at low elevations near Boston, Massachusetts, became dormant early, while southern lowland ecotypes continued growing until injured by frost. Hoffman conducted an experiment with three photoperiodic treatments and progenies of widely different seed and pollen sources. He gave examples of markedly different duration of growth for progenies of distant pollen sources under a short photoperiod, as well as of large growth responses to different photoperiods in a northern progeny. No more data were given because they did not seem sufficient for clear interpretation of the interaction results. He believed, however, that photoperiodic responses vary depending on the latitude of seed source. The very abrupt response of Alaskan seedlings under Boston photoperiods appears to justify such a belief.

Pauley & Perry (1954) grew near Boston many clones of three species of *Populus* originating from widely distant sources. The time of the termination of stem elongation was correlated with latitude of the source and, in *P. trichocarpa* Torr. & Gray from different elevations in one latitude, with length of warm season at the source. Various clones were also grown under natural days and under long days extended artificially. Confounding the photoperiods with different amounts of light was practically eliminated by using artificial light of low intensity. This was 1.5 f.c. at the ground, sufficient for photoperiodic response but too low for any significant photosynthesis. The higher the latitude or altitude of the source, the greater was the response to the treatments. As illustrated by examples, the plants with long growth periods grew much taller and developed more leaves. These data and data from crossings between latitudinally distant sources were interpreted as agreeing with the hypothesis of photoperiodic ecotypes. It was suggested that the photoperiodic response is inherited as a multiple factor character.

Karschon (1949) studied the photoperiodic responses of seedlings of *Pinus sylvestris* L. from different elevations in Switzerland. In the short day treatment, natural light was used. In the long day (15 hr) and the continuous day treatments artificial light was used. Both the photoperiods and amounts of light seem to have been different in the treatments. The possibly higher light intensity under the "short

days" may explain why the greatest height (hypocotyl length) was attained under this treatment. The effects of the treatments in height growth of seedlings from different altitudes, and of the interaction (treatment × elevation) were large and statistically significant.

Karschon also found an interesting contrast in another similar analysis. The effects of the parent trees within each seed source (elevation) were statistically significant, but small, and not interacted by photoperiodic treatments. This gives weight to his suggestion that there were photoperiodically different ecotypes at different elevations. The lower the elevation of the seed source, the greater was the growth under the short day treatment, with a linear correlation.

In Vaartaja's (1954) experiment the main light period with the high intensity (maximum 7000 f.c.) was the same for the two photoperiodic treatments and the long day was provided by continuous light of low intensity (50 f.c.). Therefore the photoperiodic treatments were not seriously confounded with differences in amount of light. The growth of Finnish seedlings of *P. sylvestris* and of *Alnus incana* (L.) Moench showed obvious interaction of photoperiods and seed sources. The northern seedlings actually grew better than southern ones under the long day. Under the short day the southern seedlings grew better. The results are strong evidence of photoperiodic ecotypes in these species. Some data indicated but with less confidence, that *Picea abies* (L.) Karst. also contained photoperiodic ecotypes.

The existence of photoperiodic ecotypes in *P. sylvestris* was also indicated by the results of Wassink & Wiersma (1955). The seedlings from northern Sweden made slightly less growth than those from France under continuous light and much less with 12-hr day. Similar results were described for southern and northern *P. taeda* L. in Florida in the preliminary report of Perry & Wu (1957).

There is evidence of lack of photoperiodic ecotypes in certain trees. Olson & Nienstaedt (1957) found that seedlings of *Tsuga canadensis* (L.) Carr from many northern and mountain sources grew much less than those from other sources regardless of various photoperiodic treatments. Critchfield (1957) noticed that the length of the growth period of *Pinus contorta* Dougl. from various sources was not dependent on the time of the year when grown in a greenhouse. According to Irgens-Moller (1957) long days hasten bud bursting in *Pseudotsuga taxifolia* (Poir.) Britton originating from high elevations, but not in those from low elevations.

The existence of photoperiodic ecotypes in annuals, especially in many cultivated plants, is better known. The interaction of seed source and photoperiod on flowering responses and vegetative elongation has recently been confirmed for many cultivated and wild grasses (Allard & Evans 1941, Olmsted 1944, Larsen 1947, McMillan 1957a).

This study is an attempt to determine whether photoperiodic variation exists within species of the

most important coniferous and deciduous genera, mainly from Europe and North America. Several photoperiodic treatments were utilized to facilitate analysis of differences between northern and southern seedlings. The treatments were arranged by alternating light and dark periods in such a manner that confounding the treatments with differences in other factors was minimized. A short summary of the main results was published earlier (Vaartaja 1957b).

METHODS

Seed samples of various tree species were collected from latitudinally distant sources. An attempt was made to use only seed collected personally, by colleagues, or qualified forestry officials, from original natural stands. In some instances commercial seed, preferably of certified origin was used. With a few exceptions the seed sources were from low elevations in continental climates. Seed of 38 species, 19 genera, and 82 origins were utilized. These are listed in the next section.

Seed was sown in 5-in clay pots in a mixture of forest humus, peat, vermiculite, and fertilized sand. Captan fungicide and Malathion insecticide were used against damping-off fungi and insect infestations. Two pots of each seed origin were subjected to four photoperiodic treatments in a greenhouse.

Sunlight, supplemented with cool, white fluorescent tubes, was utilized for the main light period during the day. Black paper or plastic covers were used to limit this period to 11 hrs. Fluorescent tubes were also used to give 1-hr light at night. The night light was given at different times as shown in Table 1. This arrangement provided different photoperiodic conditions and yet the same amount of light for all treatments. It also helped to equalize the temperature conditions. Preliminary tests indicated that tree seedlings grew in the same general way under both long and short photoperiods if the dark period that accompanied the short photoperiod was interrupted in the middle by 1 hr of light.

The intensity of the additional light at plant level was about 500 f.c. Spruce seedlings kept farther away responded to lights, indicating that the light energy received at night well exceeded the threshold for pronounced photoperiodic stimulation.

The fluorescent lights were on the north side of the rows of pots in a tilted frame so that they never shaded the plants from direct sunlight. Light intensity during the main light period varied, depending on the sun's position and on the weather; rarely it dropped to the intensity of the fluorescent light (500 f.c.); at bright mid-day it reached 5,000 to 8,000 f.c. It was the same for all treatments except at mid-winter; then frost on the wall and framework of the structure at the east and west walls of the greenhouse often shaded plants in one of the treatments. This reduction in light intensity caused a biased tendency against the photoperiodic effects. The effects of the shading may have reduced the precision and effectiveness of one of the experiments, but could not have affected the main conclusions. (This kind of diffi-

TABLE 1. Arrangement of photoperiodic treatments with one-hour light period at different times during the dark period from 5 p.m. to 6 a.m.

Treatment ¹	Supplementary light period	Duration of the longer dark period	Corresp. day-length ²	Lat. of corresp. mid-summer day ³
VSD.....	5- 6 pm	12 hr	12 hr	1°
SD.....	7- 8 pm	10 hr	14 hr	30°
LD.....	9-10 pm	8 hr	16 hr	47°
VLD.....	11-12 pm	6 hr	18 hr	56°

¹ The symbols represent very short days (VSD), short days (SD), long days (LD), or very long days (VLD).

² Assuming that the duration of the longer of two daily dark periods determines the photoperiodic response.

³ The latitude in which sun is visible for given daylength on June 21 according to Eckert & Clemence (1946).

culty would not occur in greenhouses built in east-west direction. In agreement with Lawrence (1955) it is suggested that narrow greenhouses should not be built in north-south direction.)

The air temperature in the greenhouse was thermostatically controlled. Temperature fluctuated daily, usually between 15 and 20 or 25°C. around the plants. Soil in pots was kept moist by frequent sprinkling with tap water. Thus, temperature and moisture were always at or near the supposed optimum for growth of most plants.

Observations on development of the seedlings were made several times during the experiments. The growth (top length, top weight, and root weight) of the seedlings was measured at the end of each experiment, 15 to 19 weeks after sowing. When seeds of a species were available from two distant sources, these were treated as a pair. Such pairs were placed at random in two blocks. The row of pots close to the lamps and another farther from these constituted the blocks. The difference or ratio in growth of two seed sources was considered as the basic unit for the statistical analysis. Such analysis gave a very direct estimation of the seed source-treatment interaction. The number of seedlings included in the data are given in the subsection "Individual variation."

Some of the differences between northern and southern seed sources were retested by repeating the experiments with other seed lots from the same or nearby sources. Repetitions were made with six species. The results were essentially the same as in the original experiments and will not be reported in detail. Four of the photographs (Figs. 1, 2, 3, 5) illustrate the results obtained in the repetitions.

The stable conditions of the treatments never occur in the complex natural environment which changes both cyclically and irregularly. The corresponding daylengths and the latitudes in which these daylengths occur are given in Table 1. This is over-simplified but it does illustrate the relationship between the natural daylengths and the most essential factor of the treatments. Similarly when the symbols, such as VLD ("very long day," Table 1), are used later, they refer to the artificial conditions which approach

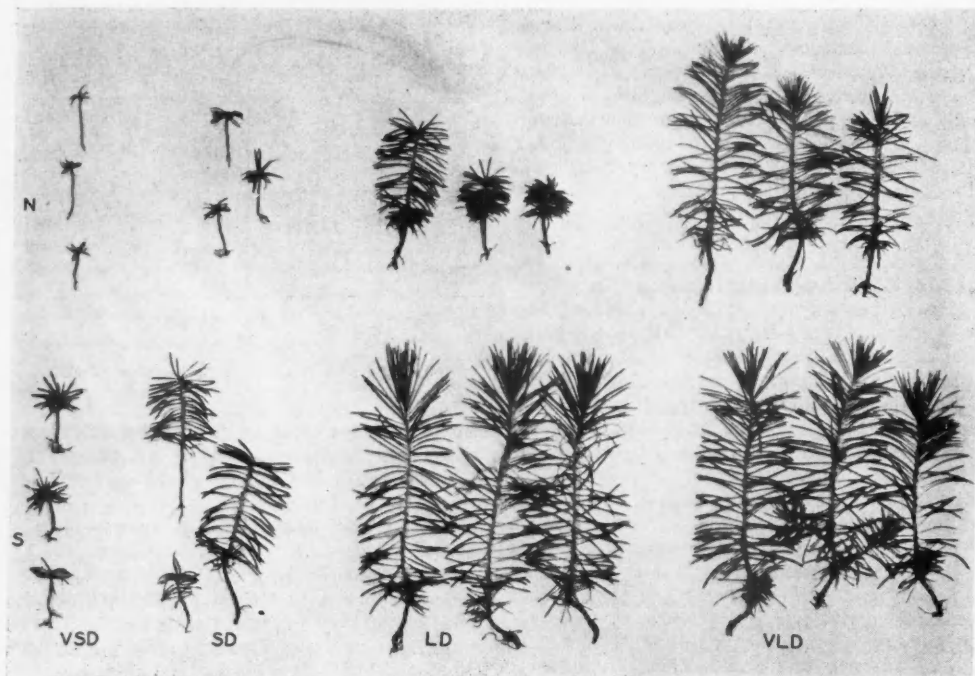


FIG. 1. Effect of photoperiods on *Larix laricina* from latitudes 60° (N, top row) and 46° (S). The smallest, average, and largest seedlings grown for 15 weeks under the four treatments described in Table 1.

natural daylength conditions only in certain essential respects.

A limited number of seedlings were also subjected to daily 8-hr light periods and to continuous light. These treatments, called the extremely short day (ESD) and the extremely long day (ELD), are discussed in detail in a special subsection.

RESULTS

RESPONSES TO PHOTOPERIODS

Most of the experimental seedlings grew slowly and soon became fully or partly dormant under the very short day (VSD). This usually resulted in short stems, short internodes, small top and root weights, and early development of terminal buds. These inhibition effects took place under the short day (SD) in some seedlings and, in a few, even under the long day (LD) (Fig. 1).

An expression of photoperiodic response is the ratio of height under VLD to that under VSD. This

ratio $\frac{VLD}{VSD}$ is used as an index of photoperiodic sensitivity.

The inhibition was observed in one form or other, in most of the following seedlings from various seed sources; the number (or numbers) following the latitude is the sensitivity index measured in an experiment (or experiments):

1. *Abies balsamea* (L.) Mill., balsam fir

(a) Wisconsin, 45°—1.0 (6.0 when calculated for weight), 2.6

(b) New York, 44°—1.8

2. *Acer negundo* L., Manitoba maple

(a) Saskatchewan, 52°—3.5, 1.4

(b) Montana, about 45°—1.4, 1.4

(c) Louisiana, 30°—1.1, 1.0

3. *A. rubrum* L., red maple

(a) Ontario, 48°—2.0

(b) Louisiana, 30°—1.2

4. *A. saccharum* Marsh., sugar maple

(a) Ontario, 46°—1.5

5. *Alnus tenuifolia* Nutt., mountain alder

(a) Saskatchewan, 54°—3.0

6. *Betula lutea* Michx. f., yellow birch

(a) Ontario, 45°—2.2

(b) Pennsylvania, 42°—2.2

7. *B. occidentalis* Hook., water birch

(a) Saskatchewan, 52°—1.4

8. *B. papyrifera* Marsh., white birch

(a) Northwest Territories, 69° (var. *humilis* (Regel) Fern. & Raup)—2.6 (186

for weight) ($\frac{ELD}{VSD} = 32$)

(b) Alaska, 64°—4.0, 2.7 ($\frac{ELD}{VSD} = 19$)

(c) Saskatchewan, 55°—6.5, 7.0 and 52°—3.0, 3.6

- (d) Manitoba, 54°—2.0
 (e) Wisconsin, 46°—5.7
 (f) Pennsylvania, 42°—1.6
9. *Caragana arborescens* Lam., caragana
 (a) Saskatchewan (origin in Asia not known)—2.4
10. *Casuarina equisetifolia* L.
 (a) California (origin in Australia about 20°¹)—1.1
11. *Cupressus arizonica* Greene, Arizona cypress
 (a) Arizona, about 33°—0.6
12. *Fraxinus americana* L., white ash
 (a) Utah (origin not known)—1.2, 1.2
13. *F. pennsylvanica* Marsh. var. *subintegerrima* (Vahl) Fern., green ash
 (a) Saskatchewan, 52°—1.8, 1.2
 (b) Montana, 45°—1.2
 (c) Georgia, 33°—1.3, 0.8
14. *Larix laricina* (Du Roi) K. Koch, tamarack
 (a) Northwest Territories, 60°—H($\frac{VLD}{SD}$) = 4.9), 2.4
 (b) Manitoba, 54°—6.3
 (c) Saskatchewan, 53°—3.8
 (d) Wisconsin, 46°—5.8, 3.1
15. *Picea abies* (L.) Karst., Norway spruce
 (a) Sweden, about 57°—3.7
 (b) Germany, 50°—2.1
16. *P. engelmannii* Parry, Engelmann spruce
 (a) British Columbia, 51°—2.2
17. *P. glauca* (Moench) Voss, white spruce
 (a) Yukon, 63°—1.2
 (b) Northwest Territories, 60°—2.4, 1.7
 (c) Saskatchewan, 54°—(1.1) ?
 (d) Wisconsin, 46°—2.7, 2.4
 (e) Quebec, 48°—2.9
18. *P. mariana* (Mill.) B.S.P., black spruce
 (a) Northwest Territories, 61°—1.6 (8.9 for weight)
 (b) Labrador, 52°—1.9
 (c) Wisconsin, 44°—5.8
 (d) Pennsylvania, 42°—3.0
19. *P. rubens* Sarg., red spruce
 (a) Quebec, 45°—2.0
 (b) Nova Scotia, 45°—1.5
 (c) New Hampshire, 44°—1.6
 (d) New York, 41°—1.6
 (e) West Virginia, 39° (high elevation ?)—1.9
20. *P. sitchensis* (Bong.) Carr, Sitka spruce
 (a) Alaska, 60°—2.2
 (b) Oregon, 43°—1.2
21. *Pinus banksiana* Lamb., jack pine
 (a) Northwest Territories, 60°—1.3
 (b) Saskatchewan, 55°—1.3
 (c) Wisconsin, 46°—1.6
22. *P. contorta* Dougl. var. *latifolia* Engelm., lodge-pole pine
 (a) British Columbia, 53°—2.1
23. *P. ponderosa* Laws., ponderosa pine
 (a) British Columbia, 51°—1.7
24. *P. radiata* D. Don., Monterey pine
 (a) California, 36°—0.8
25. *P. resinosa* Ait., red pine
 (a) Ontario, 46°—1.3
 (b) Pennsylvania, 42°—1.2
 (c) Nova Scotia, 43°—1.2
26. *P. rigida* Mill., pitch pine
 (a) New York, 44°—1.4
 (b) North Carolina, 35°—1.3
27. *P. strobus* L., eastern white pine
 (a) Ontario, 46°—1.4
 (b) North Carolina, 35°—1.3, 1.4
28. *P. sylvestris* L., Scots pine
 (a) Finland, 60°—1.8, 1.6
 (b) England, 52°—1.4
 (c) Spain, 41°—1.5, 1.2
29. *Platanus occidentalis* L., sycamore
 (a) Ohio, 40°—1.7
 (b) Louisiana, 31°—1.1, 0.8
30. *Pseudotsuga taxifolia* (Poir.) Britton, Douglas fir
 (a) British Columbia, 50°—1.5
 (b) Oregon, 43°—1.1
31. *Quercus macrocarpa* Michx., bur oak
 (a) Manitoba, 50°—1.1 (the buds under VLD were about to burst at the time of recording)
32. *Sequoia sempervirens* (D. Don) Endl., redwood
 (a) California, 37°—1.0
33. *Tilia americana*, basswood
 (a) Ontario, 46°—1.1 (Seedlings under VSD were thin and died just before the time of recording)
34. *Thuja occidentalis* L., eastern white cedar
 (a) Ontario, 44°—1.2
 (b) Manitoba, 50°—0.9
 (c) Wisconsin, 45°—1.1
35. *T. plicata* Donn, western red cedar
 (a) Alaska, 58°—1.2
 (b) Oregon, 46°—1.1
36. *Tsuga canadensis* (L.) Carr., eastern hemlock
 (a) Ontario, 45°—3.3
 (b) Pennsylvania, 42°—1.4
37. *T. mertensiana* (Bong.) Carr., mountain hemlock
 (a) Alaska, 60°—1.1
 (b) Oregon, 44°—1.1
38. *Ulmus americana* L., white elm
 (a) Saskatchewan, 51° and 52°—1.3 (2.3) and 1.2
 (b) Nebraska, 41°—1.7, 1.5

¹ Southern latitude; all the others are northern latitudes. In the discussion of this study only the northern hemisphere is considered. Of course the analogous situation may occur in the southern hemisphere but no data are yet available on the photoperiodic responses of trees of the southern hemisphere.

As this list of 82 sources shows, the index for photoperiodic sensitivity had a tendency to be larger than 1.0, often much larger. This means that most seedlings grew larger under long than under short days. Several of the exceptions were more apparent than real. For instance, species of certain

genera such as *Abies*, *Quercus*, *Tilia*, *Tsuga*, far northern *Larix*, far northern *Picea*, and far northern *Betula* soon formed terminal buds and ceased elongating for a while, or elongated very slowly. The weight data showed, however, that these made more growth under long days. Some seedlings later resumed terminal growth under VLD or ELD. Furthermore, in many far northern seedlings prolonged growth took place only if the daylength was extremely long (ELD, Fig. 2).

Truly exceptional were most seedlings from far southern sources such as *Acer* spp. (those from Louisiana), *Casuarina*, *Cupressus*, *Fraxinus* spp. (from Georgia), *P. radiata*, *Platanus* (from Louisiana), and *Sequoia*. These either did not respond to the treatments with relatively long days (VLD, LD, SD, VSD) or they are not at all responsive photoperiodically. The same was true with species of *Thuja*, these being the only northern species tested with no or little inhibition by VSD.

Table 2 shows the responses in seedlings selected to represent most of the genera and the far distant origins tested. The responses in seedlings from latitudinally distant origins are also illustrated in Fig. 1 to 5. In addition to the species not considered sensitive (Group V), the seedlings of Table 2 were classified into the following groups.

The northern seedlings (I), from latitudes 54 to 60°, were characterized by great sensitivity to the treatments, and by a tendency toward the critical daylength being LD. As a contrast to these the southern seedlings (III) from latitudes 33 to 41° were less sensitive and the critical daylength tended to be VSD. Group II was intermediate.

In the maritime group (IV) the critical daylengths appeared to be shorter than in the seedlings from continental climates of the same latitudes.

Although the maximum inhibition nearly always occurred under VSD, the best growth was under either VLD or LD (Table 2). An explanation of this may be that there is an optimal daylength which for certain trees is not necessarily very long. The growth was fair or good under LD and VLD even for all the southern seedlings tested.

The main purpose of Table 2 is to illustrate the actual photoperiodic growth responses (see also Fig. 1 to 5). In most of the following sections these will not be given. Instead attention will be focused on the differences (or ratios) between seedlings from different origins within each species.

Table 2 demonstrates that the photoperiodic responses fall in different patterns even in intergeneric comparisons. If the few nonresponsive species are ignored, there appears to be a general rule: the farther north the origin, the greater is the photoperiodic sensitivity (see also indices in the list above) and the longer is the critical daylength. This may be true because there are photoperiodic differences between the northern and southern genera or between species within genera or between ecotypes within species or between all these. The hypothesis on the ecotypes is the main concern in the following sections.

TABLE 2. Growth responses of tree seedlings to daylength. Examples of various genera from widely distant latitudes.

Species	Lat. of source	VSD ¹	SD	LD	VLD	Sensitivity ($\frac{\text{VLD}}{\text{VSD}}$) ³
		Height, ² mm				
I. Northern continental						
<i>Pinus sylvestris</i>	60°	27	32	34 ⁴	49	1.8
<i>Larix laricina</i>	60°	(died)	13	13	64	(4.9)
<i>Picea abies</i>	57°	12	13	16	42	3.7
<i>Alnus tenuifolia</i>	54°	16	12	21	45	3.0
II. Southern continental						
<i>Ulmus americana</i> ...	41°	63	93	98	105	1.7
<i>Pinus strobus</i>	35°	66	92	97	86	1.3
<i>Pinus rigida</i>	35°	59	70	73	77	1.3
<i>Fraxinus pennsylvanica</i> var. <i>sub-integrifolia</i>	33°	68	81	95	89	1.3
III. Intermediate						
<i>Picea mariana</i>	52°	17	16	31	33	1.9
<i>Acer negundo</i>	52°	41	65	125	142	3.5
<i>Acer rubrum</i>	48°	49	70	107	100	2.0
<i>Picea glauca</i>	46°	30	55	91	81	2.7
<i>Tsuga canadensis</i> ...	42°	14	14	20	20	1.4
<i>Betula lutea</i>	42°	22	24	54	49	2.2
IV. Maritime						
<i>Picea sitchensis</i>	60°	20	23	60	42	2.2
<i>Pseudotsuga taxifolia</i>	50°	71	109	120	107	1.5
<i>Pinus resinosa</i>	43°	35	42	53	47	1.3
V. Insensitive						
<i>Thuja plicata</i>	58°	55	65	69	64	1.2
<i>Thuja occidentalis</i> ...	56°	47	49	53	52	1.1

¹ Daylength treatments; see Table 1.

² Average distance from root collar to tip of stem after 15 to 19 weeks growth.

³ Ratio of height under very long day to height under very short day ($\frac{\text{VLD}}{\text{VSD}}$).

⁴ Values in boldface type show the critical daylength, i.e., the maximum day under which there was a clear growth inhibition.

INTERACTION OF SEED SOURCES AND TREATMENTS

EXAMPLES

Two general methods were used in demonstrating interaction of seed source and photoperiod. They were: (1) differences in terminal dormancy between the seed sources under different treatments; (2) differences in growth ratios of two sources under different treatments.

1. *Differences in terminal dormancy.*—Early cessation of stem elongation (terminal dormancy) commonly took place under certain treatments. The longest day under which this happened for certain seedlings may be called the critical daylength (for elongation). If the critical daylengths appeared to be the same for all sources to be compared, no interaction was suggested but if they were different an interaction was suggested. This is illustrated by the following example with *Larix laricina*. After 19 weeks' growth, the following percentages of the seedlings under each of the 4 treatments exhibited terminal dormancy:

Source	Lat.	VSD	SD	LD	VLD
Manitoba	54°	100	93	0	0
Wisconsin	46°	100	63	0	0

The critical daylength (boldface type) was the same for both populations although not for all individuals in these. These data were not considered as conclusive evidence of interaction, although the different percentages under SD suggest a difference, as would be expected according to the hypothesis. This test was repeated with seed from Wisconsin and N.W.T. (latitude 60°). The results with Wisconsin seedlings agreed with those above (Fig. 1). For the N.W.T. seedlings the critical daylength was LD, a longer one than for the Wisconsin seedlings, as would be expected.

In presenting data of this type below, the percentages are omitted; instead, — or + signs are given to show whether less or more than half of the seedlings were dormant. In most cases the percentages were either 0 or 100 or close to these.

2. *Differences in growth ratios.*—Many comparisons were made between two (northern and southern) seed sources of a species. In these the paired quantitative growth data, such as two heights, could be reduced to one ratio; the value for northern source (N) was divided by that for southern source (S). This

ratio $\frac{N}{S}$ is usually below 1.0, which may be a result of small seeds, slow germination, and growth rate, as well as of intrinsic tendency to terminate growth early in northern sources. If this ratio is different from one treatment to another, an interaction of the seed sources and the treatment is indicated.

Utilizing the growth ratios reduces the data to be dealt with and gives a direct estimate of the interaction. A difference (S-N) could be used but the ratio also offers the advantage that data from fast growing species are more comparable with those from slow ones.

This method of presentation is illustrated for seedlings of *Betula papyrifera* as follows. The average fresh weights of the tops were (in mg, after 15 weeks' growth):

Source	Lat.	VSD	SD	LD	VLD
N.W.T.	69°	2	8	155	372
Pennsylvania	42°	93	110	133	209

When, in each column, the value of N.W.T. is divided by that of Pennsylvania, the following weight ratios are obtained:

N.W.T.	VSD	SD	LD	VLD
Pa.	0.02	0.07	1.17	1.78

The large differences in these ratios are interpreted as indicating marked interaction of seed source and daylength, as expressed in top growth. Under long days the northern source grew better and under short days the southern source grew better. The sharp drop in the ratios from LD to SD shows that SD was critical for top growth of N.W.T. (see also Fig. 2). This drop was unusually sharp and demonstrated the extreme sensitivity of this seed source to photoperiods. This sensitivity was often observed in attempts to get

birch seedlings of various northern origins to grow under VSD.

The following data illustrate the same ratio procedure for the root weight of the same seedlings of *B. papyrifera* (mg., fresh):

	Lat.	VSD	SD	LD	VLD
Pennsylvania	42°	63	78	44	75
N.W.T.	69°	3	4	205	600
Ratio	$\frac{\text{N.W.T.}}{\text{Pa.}}$	0.05	0.05	4.66	8.00

Interaction was again demonstrated, the ratios being very different under different daylengths. SD was critical for root growth of N.W.T. seedlings (see also Fig. 2).

The N.W.T. *B. papyrifera*, which in its northwestern range is considered to belong to the geographic variety *humilis*, was from its extreme northern limit at Aklavik (lat. 68° 40'). This fact, together with the general sensitivity of northern *Betula*, explains the large differences in the above ratios. No comparable differences were found with seedlings from less northerly sources.

The numbers of lateral buds of N.W.T. seedlings of *B. papyrifera* were about 6 times those of Pennsylvania seedlings under both VLD and LD. The N.W.T. seedlings had no buds under SD and VSD (see also Fig. 2).

These data indicate very fast development of top, roots, and lateral buds of extreme northern *B. papyrifera* under VLD and LD. However, the stems were short (Table 7), giving the seedlings a rosette appearance (Fig. 2). This may be a normal characteristic of these northern trees which are known to have a shrubby low form on their natural sites. Even VLD was not long enough to allow full terminal elongation, yet allowing otherwise good growth especially for roots. This was shown in a comparison under ELD (continuous light); the seedlings from N.W.T. elongated normally and as fast as southern seedlings (Fig. 2).

Most of the data of this study will be given as growth ratios similar to those above. The growth values themselves will be omitted because of their large number and because they are less interesting for seedlings from less northerly sources.

TERMINAL DORMANCY

In the data for *Larix laricina*, discussed above, the critical daylength for terminal dormancy was SD for Manitoba and Wisconsin seed sources and LD for N.W.T. source. Difficulty was experienced when placing some of these seedlings, as well as seedlings of some other species, in dormant or non-dormant classes. The seedlings sometimes were in a semi-dormant state and elongated very slowly. When this occurred, the lateral development was not inhibited and the seedlings had a rosette appearance. In *Betula* this was common (Fig. 2), and therefore no data were collected on dormancy. Similarly no dormancy data were collected for *Thuja plicata*, which apparent-

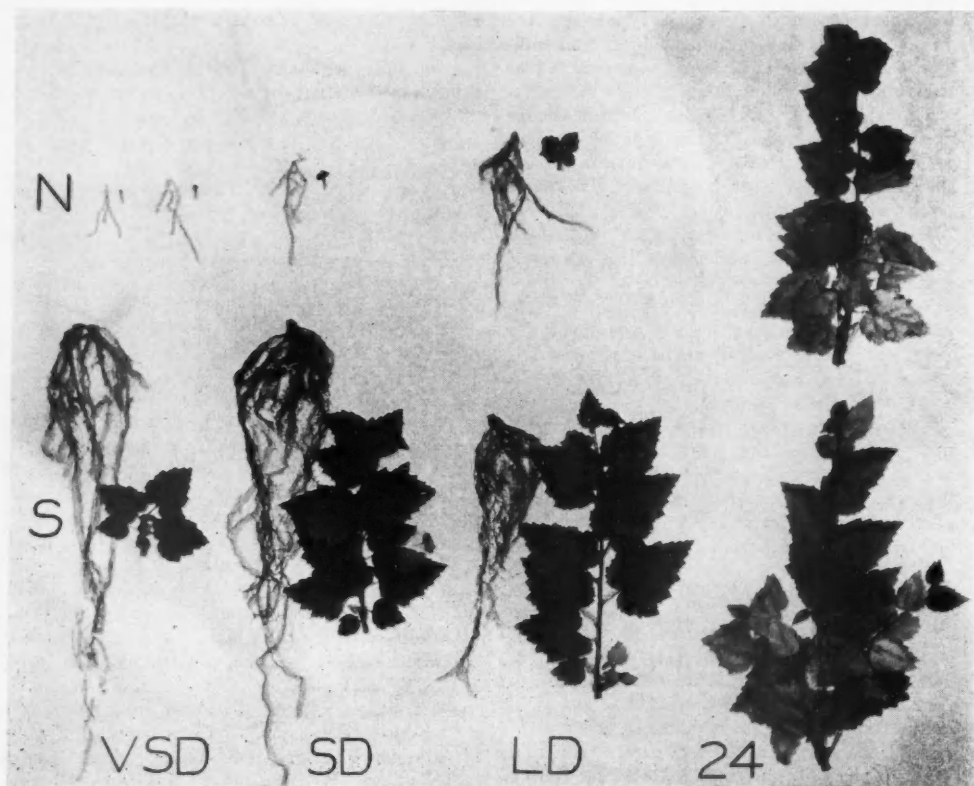


FIG. 2. Effect of photoperiods on *Betula papyrifera* from latitudes 69° (N, top row) and 52° (S). Dominant seedlings grown for 15 weeks under three of the treatments described in Table 1 and under continuous light (24). The root systems were extensive for both sources under continuous light.

ly grew all the time even under VSD. In most genera the formation of swollen terminal buds (or analogous structures at the tip) offered a sign of the cessation of elongation.

The seedlings of *Pinus resinosa* from two sources continued elongating for at least 10 weeks under all treatments. After 14 weeks they all ceased elongating and formed terminal buds under all treatments.

TABLE 3. Interaction of photoperiod and seed source. Response in development of terminal buds of *Pinus banksiana* seedlings grown in greenhouse.

Age (weeks)	Lat.	VSD ¹	SD	LD	VLD
		Bud ² present (+) or absent (-)			
10	60°	+	+	+	-
	54°	+	+	-	-
	45°	+	-	-	-
14	60°	+	+	+	+
	54°	+	+	+	+
	45°	+	+	+	-

¹ Daylength treatments; see Table 1.

² Occurrence of terminal buds in the majority of seedlings.

Similarly, seedlings of many other *Pinus* species formed terminal buds after 14 weeks regardless of the treatment. Nevertheless there were long periods when an interaction of sources and treatments was observed. This is illustrated for *P. banksiana* in Table 3. Each of the three sources responded differently to the daylength treatments.

Table 4 shows similar interaction for three other species of *Pinus*. A few seedlings of the southern sources of *Pinus*, especially of *P. rigida*, started to elongate again after forming a small temporary terminal bud. Similar periodicity took place occasionally in other genera and species. At the end of the experimental period it appeared that a new period of elongation was about to start in some dormant individuals of various species of *Pinus*. After that it would have been difficult to compare the dormancy of different origins in the simple manner shown in the tables.

Table 5 shows interaction for dormancy of species of *Picea* (see also Fig. 3 and 4). To simplify the presentation, only one period showing differences between the sources is included for each species. These data are from different, but closely related, spe-

TABLE 4. Interaction of photoperiod and seed source. Response in development of terminal buds of seedlings of three species of *Pinus* grown in greenhouse.

Species	Age (weeks)	Lat.	VSD ¹	SD	LD	VLD
			Bud ² present (+) or absent (-)			
<i>P. sylvestris</i>	10	60°	+	+	+	-
	10	41°	-	-	-	-
<i>P. sylvestris</i>	14	60°	+	+	+	+
	14	41°	+	+	-	-
<i>P. strobus</i>	8	49°	+	+	-	-
	8	35°	-	-	-	-
<i>P. strobus</i>	15	49°	+	+	+	+
	15	35°	+	+	-	-
<i>P. rigida</i>	10	44°	+	-	-	-
	10	35°	-	-	-	-
<i>P. rigida</i>	14	44°	+	+	-	-
	14	35°	+	-	-	-

¹ Daylength treatments; see Table 1.² Occurrence of terminal buds in the majority of seedlings.

cies and from two separate, but identical, experiments. Therefore, a rough comparison may be made not only between the pairs indicated but with all the data in the table. Only the maritime *P. sitchensis* does not appear comparable with the other seedlings from the same latitudes. Other seedlings showed a general correlation: the farther north the seed source, the longer are the days inhibiting elongation.

Table 6 shows interactions for the four remaining species for which the elongation was recorded.

The data treated in this section show the same tendency for a number of tree species; in paired comparisons the critical daylength inhibiting elongation was longer for the more northern of two origins. In no case was the opposite result found. For *Pinus resinosa* there was no trend in either direction.

HEIGHT

Ratios of heights were calculated for the same pairs of seedlings as in Tables 3 to 6. The method was illustrated in an example above. When summarizing the results in Table 7, the species are given in order of descending latitudes of the northern seed sources of each two being compared. The general results are also illustrated in the photographs in Figs. 1 to 5.

It is believed that if a treatment with still longer daylength than VLD had been given, the heights of northern seedlings of the two first species would have been much greater and the ratios higher. Seedlings of these species elongated very rapidly in a separate test under continuous light (Fig. 2). Therefore, VLD

TABLE 5. Interaction of photoperiod and seed source. Response in development of terminal buds of seedlings of *Picea* species grown in greenhouse.

Species	Age (weeks)	Lat.	VSD ¹	SD	LD	VLD
			Bud ² present (+) or absent (-)			
<i>P. abies</i>	12	57°	+	+	+	-
		50°	+	+	-	-
<i>P. glauca</i>	15	60°	+	+	+	-
		54°	+	+	-	-
<i>P. mariana</i> (Expt. I)	10 to 15	61°	+	+	+	+
		44°	+	+	-	-
<i>P. mariana</i> (Expt. II)	8 to 11	52°	+	+	+	-
		41°	+	-	-	-
<i>P. rubens</i>	8 to 11	45°	+	+	-	-
		39°	+	-	-	-
<i>P. sitchensis</i> ³	6 to 15	60°	+	+	-	-
		43°	-	-	-	-

¹ Daylength treatments; see Table 1.² Occurrence of terminal buds in the majority of seedlings.³ Maritime origins.

TABLE 6. Interaction of photoperiod and seed source. Response in development of terminal buds of various tree seedlings grown in greenhouse.

Species	Age (weeks)	Lat.	VSD ¹	SD	LD	VLD
			Bud ² present (+) or absent (-)			
<i>Ulmus americana</i>	9	51°	+	+	-	-
		41°	-	-	-	-
<i>Fraxinus pennsylvanica</i> var. <i>subintegerrima</i>	12	52°	+	+	-	-
		33°	-	-	-	-
<i>Acer negundo</i>	11 to 15	52°	+	-	-	-
		45°	-	-	-	-
<i>Pseudotsuga taxifolia</i> ³	11 to 15	50°	+	-	-	-
		43°	-	-	-	-

¹ Daylength treatments; see Table 1.² Occurrence of large terminal buds in the majority of seedlings.³ Maritime origins.

was considered as the critical daylength for the far northern *B. papyrifera* and *P. mariana*. These were strongly inhibited under VLD as compared to their southern counterparts and this is expressed by the low ratios.

In table 7 the underlined values (showing the treatments critical to northern seedlings) follow a trend from VSD in southern seedlings towards VLD in

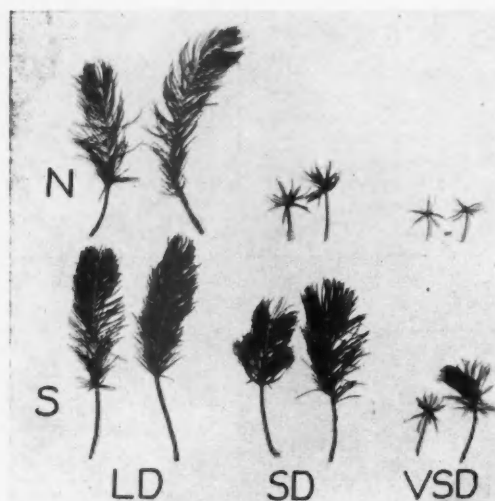


FIG. 3. Effect of photoperiods on *Picea glauca* from latitudes 60° (N, top row) and 46° (S). Dominant seedlings grown for 15 weeks under three of the treatments described in Table 1.

TABLE 7. Interaction of photoperiod and seed source. Ratio of stem height of seedlings from northern and southern sources.

Species	Lat. of source	RATIO NORTHERN/SOUTHERN				Max. diff. ²
		VSD ¹	SD	LD	VLD	
Continental:						
<i>B. papyrifera</i>	69° 42°	.22	.25	.30	.36³	.14
<i>P. mariana</i>	61° 44°	.81	.28	.32	.22	.59***
<i>P. glauca</i>	60° 53°	.92	.85	1.25	1.48 ⁴	.63***
<i>P. banksiana</i>	60° 45°	.85	.71	.71	.87	.16*
<i>P. sylvestris</i>	60° 41°	.55	.49	.52	.68	.19*
<i>L. laricina</i>	54° 46°	.86	.37	.92	.88	.55***
<i>P. mariana</i>	52° 42°	1.08	.48	.47	.73	.60***
<i>A. negundo</i>	52° 45°	.43	.41	.66	1.10	.69***
<i>U. americana</i>	51° 41°	.65	.35	.46	.44	.30*
<i>P. resinosa</i>	46° 42°	.91	.96	1.11	.98	.20
<i>P. rubens</i>	45° 39°	.93	.84	.99	1.02	.18
<i>P. rigida</i>	44° 35°	.74	.90	.90	.80	.16*
Maritime:						
<i>P. sitchensis</i>	60° 43°	.28	.27	.91	.91	.63***
<i>T. plicata</i>	58° 46°	.89	.99	.98	1.07	.18
<i>P. latifolia</i>	50° 43°	.74	1.04	1.27	1.02	.53**

¹ Daylength treatments; see Table 1.

² Difference between the highest and lowest ratios. Probability levels: *** 0.01; ** 0.05; * 0.3.

³ Values in boldface type are the daylengths critical to northern seedlings.

⁴ The high level of these particular ratios was due to the slow germination of the southern seeds.

northern seedlings. This indicated again that, even in intergeneric comparisons, the farther north the seed source, the longer is the critical daylength.

Under VSD even southern sources were inhibited and the heights of the seedlings were not much greater than those of northern seedlings. Therefore, the ratios were relatively high for many species. This took place in all except the maritime species and a few

of the southernmost ones, for which even VSD was not inhibitive.

Where the ratios differed significantly from one treatment to another within a species, interaction of the treatments and the two seed sources was indicated. This indication was strong (marked ** and ***) in 7 pairs of sources, weak (marked *) in 4, and lacking in 4. In *Betula papyrifera* no interaction was apparent because the longest day tested was too short for the extremely northern source. *Thuja plicata* seedlings did not respond to the treatments at all, or the response was very small (Table 1). It is difficult to reject the possibility of interaction on the basis of these results in *Picea rubens* and *Pinus resinosa* for the reasons that follow: the distances between the northern and southern sources were small; other species had strong interactions and thus caused relatively large variation and large experimental error in the design used; to demonstrate the interactions of these two species a more refined design or more replications may be necessary.

The interactions, as expressed in the column at the extreme right of Table 7, were relatively small for species of *Pinus*. This agrees with the observations on terminal dormancy (Tables 3, 4). The pines showed differences in dormancy during only a limited period, before becoming dormant regardless of the treatments. Therefore, no such great height differences were shown by pines as were shown for instance by some spruces.

Separate experiments were conducted with three more species without statistical analysis. Since the experimental conditions were much the same as for Table 7 and the results followed the same pattern, these should be of some significance. The ratios for heights are given below:

Species	Lat.	VSD	SD	LD	VLD
<i>Picea abies</i>	57° 50°	0.96	0.97	0.60	1.12
<i>F. pennsylvanica</i>					
var. <i>subintegerrima</i>	52° 33°	0.59	0.69	0.69	0.90
<i>Pinus strobus</i>	46° 35°	0.49	0.54	0.88	0.80

The data (see also Fig. 4) suggested that similar interaction took place in these species as in most species in Table 7, that is, the critical daylength that greatly inhibited height growth was longer for the more northern of two origins.

WEIGHT

Ratios of the fresh weights of the tops of seedlings (stem + leaves) are given in Table 8 in the same manner as the height data in Table 7. Generally the results agreed with the results on stem lengths. The underlined critical points again suggest a general correlation with latitudes, but the pattern is more irregular. There are also other irregularities in the individual values. These irregularities might be explained by assuming that growth of the entire top may be controlled by photoperiods through a less direct mechanism than height growth.

The strong interaction for top weight of *B. papyrifera* has already been discussed. For *P. rubens* and

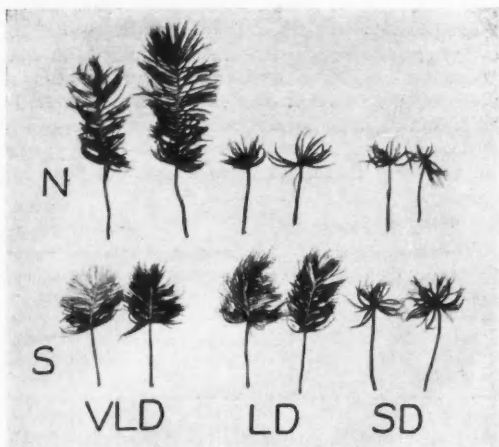


FIG. 4. Effect of photoperiods on *Picea abies* from latitudes 57° (N, top row) and 50° (S). Dominant seedlings grown for 17 weeks under three of the treatments described in Table 1.

T. plicata the data on weight, in contrast to height, gave some suggestion of interaction. The results for *P. rubens* is as might be expected, considering the general pattern of the ratios, with a pronounced depression in ratios under SD (critical daylength). On the other hand, there is a high ratio for *T. plicata* under SD where a depression would be expected (compare with *P. sitchensis*). Therefore, the suggestion for *P. rubens* appears to reflect a real interaction and for *T. plicata* perhaps only an experimental accident.

Analysis of the root weights revealed general tendencies roughly similar to those in Tables 7 and 8. The interactions, however, were often inconsistent, usually small, and not significant. It seems, as was shown earlier with northern *B. papyrifera*, that root growth was not always retarded under the same treatments that retarded stem elongation. If this is true in general, it would offer advantages to plants. The roots could safely function during short days towards the end of the growing season, being located in an environment better protected than that of tops. The situation is complicated, however, because the full activity of the roots must depend on the assimilation products from the tops. The most consistent results were obtained with *P. sitchensis*, the root weight ratios being as follows:

Latitudes	VSD	SD	LD	VLD
60° 43°	.22	.24	1.26	1.08

For this species the critical daylength was the same for tops and roots.

LATERAL DEVELOPMENT

Analysis of the lateral development was difficult because of differences in the species studied. Some soon branched profusely, while others formed many lateral buds but no branches. Many species had no

TABLE 8. Interaction of photoperiod and seed source. Ratio of top weight of seedlings from northern and southern sources.

Species	Lat. of source	RATIO NORTHERN/SOUTHERN				Max. diff. ²
		VSD ¹	SD	LD	VLD	
Continental:						
<i>B. papyrifera</i>	69° 42°	.01	.12 ³	1.17	1.78	1.77***
<i>P. mariana</i>	61° 44°	.70	.96	.22	.11	.59**
<i>P. glauca</i>	60° 53°	1.34	1.00	.42	.71	.92***
<i>P. banksiana</i>	60° 45°	.57	.56	.56	.67	.10
<i>P. sylvestris</i>	60° 41°	.43	.29	.30	.60	.31*
<i>L. laricina</i>	54° 46°	.69	.72	.95	.99	.27*
<i>P. mariana</i>	52° 42°	.68	.12	.15	.48	.53**
<i>A. negundo</i>	52° 45°	.28	.32	.37	1.10	.78***
<i>U. americana</i>	51° 41°	.43	.14	.22	.18	.29*
<i>P. resinosa</i>	46° 42°	.85	.77	.76	.75	.10
<i>P. rubens</i>	45° 39°	.41	.35	.80	.76	.41*
<i>P. rigida</i>	44° 35°	.60	1.17	.82	.61	.51*
Maritime:						
<i>P. sitchensis</i>	60° 43°	.05	.09	1.09	.86	1.00***
<i>T. plicata</i>	58° 46°	.73	1.02	.81	.82	.29*
<i>P. latifolia</i>	50° 43°	.73	.95	1.28	.95	.55**

¹ Daylength treatments; see Table 1.

² Difference between highest and lowest ratios. Probability levels: *** 0.01; ** 0.05; * 0.3.

³ Daylength critical to northern seedlings in boldface type.

such lateral development at all under certain treatments. The only way to analyze the data was to omit VSD and to deal with the combined number of buds and branches. However, only branches were included for *T. plicata* because of the prolific branching. The results are shown in Table 9 (see also Fig. 1 to 4).

There was a general tendency for the ratios to be low under SD and high under LD or VLD. This tendency is more obvious if the results under VSD are considered. This treatment allowed very little or no lateral development for most northern seedlings. The ratios of *T. plicata* did not follow the same pattern as those of other species and the differences may have been due to experimental error rather than to actual interaction.

Acer negundo formed lateral buds but did not branch during the experiment (Fig. 5). For this species, the numbers of the leaves were also counted. The ratios for these (for the sources from Saskatchewan and Montana) were:

Latitudes	VSD	SD	LD	VLD
52° 44°	.46	.54	.74	.73

Existence of interaction and the critical daylength under SD were suggested by these data.

MORPHOLOGY

The maximum daylength that fully or partially inhibited elongation often allowed rapid formation of buds, leaves, branches, and radial growth of stem. This resulted in a distortion of the relative dimensions of the seedlings and in a rosette form. In northern seedlings such rosetting took place under longer days than in southern seedlings (Figs. 1, 2, 5).



FIG. 5. Effect of photoperiods on *Acer negundo* from latitudes 52° (N, top row), 45° and 30° (S, bottom row). Dominant seedlings grown for 13 weeks under the four treatments described in Table 1, under 8-hour light (8), and under continuous light (24).

Rosetting is an expression of a tendency toward relatively greater inhibition in vertical than in lateral development. In a less conspicuous form this tendency was found even in the completely dwarfed seedlings of *Picea*. Under a critical daylength these seedlings formed apical buds soon after germination. The buds seemed normal at first but later swelled enormously and attained an abnormally broad shape. In many seedlings side buds also appeared, which does not normally happen in small seedlings. In some cases a side bud grew unproportionally large, even larger than the apical bud. Occasionally the side bud burst and formed a branch although the main axis did not elongate. These abnormalities were not recorded in detail. They occurred in most species tested and the critical daylength causing them was longer in the northern sources.

The first leaves in *A. negundo* were simple with smooth margins or with a few dents. Later leaves had incised margins and still later ones were divided or compounded. This development was suppressed by short days. The critical daylength for each degree of the suppression appeared to be the longer the farther north was the seed source (Fig. 5).

INDIVIDUAL VARIATION

The data considered above were based on the averages from a number of seedlings in each of the 8

pots of each seed source. For certain species, only a few seedlings could be left in a pot because of the severe competition due to their size and growth rate. When the seedling stand in a pot was thinned, the obviously diseased individuals were removed first. In early thinnings those individuals from unusually early or late germination were also discarded. Otherwise, thinning was performed so as to provide favorable spacing.

TABLE 9. Interaction of photoperiod and seed source. Ratio of the combined number of lateral buds and branches in seedlings from northern and southern sources.

Species	Lat. of source	RATIO NORTHERN/SOUTHERN			Max. diff. ²
		SD ¹	LD	VLD	
Continental:					
<i>B. papyrifera</i>	69° 42°	0 ³	6.13	6.00	6.13 ⁴
<i>P. mariana</i>	61° 44°	0	.71	.13	.71*
<i>P. glauca</i>	60° 53°	.82	.51	.81	.31
<i>P. banksiana</i>	60° 45°	.84	1.37	1.50	.66*
<i>P. sylvestris</i>	60° 41°	.22	.29	.53	.24
<i>L. laricina</i>	54° 46°	.22	.82	.65	.43
<i>P. mariana</i>	52° 42°	.01	.19	1.00	.99**
<i>A. negundo</i>	52° 45°	.33	.36	.66	.33*
<i>P. rubens</i>	45° 39°	.59	.99	.94	.40*
<i>P. rigida</i>	44° 35°	.73	.90	1.47	.74*
Maritime:					
<i>P. sitchensis</i>	60° 43°	.09	.34	.77	.68*
<i>T. plicata</i>	57° 46°	1.87	1.43	1.40	.47*

¹ Daylength treatments; see Table 1. VSD omitted because of many zero values.

² Difference between highest and lowest ratios. Probability levels: ** 0.05; * 0.3.

³ Daylength critical to northern seedlings in boldface type.

⁴ This species not included in the analysis.

It was desirable to base the data on a large number of individuals and to study the variation itself in as large a sample as possible. Therefore, for each species, the number of seedlings was chosen considering their size and growth rate under the most favorable treatment. Very large numbers, possible with very small species, were not used. Only for one seed source, *P. mariana* from Labrador, was no thinning made; yet about 70 of these seedlings left in each pot showed less individual variation than did the 5 seedlings left for *A. negundo*. Because of the possible occurrence of undetectable root rots, a few more seedlings than the number fixed for a species were usually grown as a reserve. When the experiment was finished and root rots observed, the extra seedlings were discarded. If the roots were healthy, the smallest seedlings were discarded.

The number of seedlings per pot that were finally studied were: *Betula* 3, *Acer* 5, *Ulmus* 7, *Larix* 8, *Pinus* spp. 12 to 15, *Pinus resinosa* 45, and other species 16 to 30. The numbers were considered large enough to study the variation of height and stem weight within each sample in 8 species.

The variation was measured as the ratio of the maximum to the average value within the fixed number of seedlings. Variation upwards from the average was considered more important than variation

downwards. This measure of variation minimized the undue influence of low values which might be caused by root diseases. Expressing the variation as a ratio made the variation of big seedlings comparable to that of small ones. The variation data, which again were in pairs (for northern and southern

sources), were reduced to the ratios $\frac{N}{S}$.

An example with *P. sitchensis* may illustrate the procedure and the results. The relative variation values for the top weights of seedlings were as follows (averages of 2 samples, 20 to 22 seedlings in each):

Source	Lat.	VSD	SD	LD	VLD
Alaska	60°	1.5	3.4	2.5	1.7
Oregon	43°	2.0	1.9	1.7	1.7
Ratio Al/Ore		.8	1.8	1.5	1.0

The ratio was high under SD because a few Alaskan seedlings grew fairly well while most were inhibited. Table 10 gives the daylengths with the maximum ratios for 8 species studied. Fig. 1, which shows seedlings of *L. laricina* from N.W.T. and Wisconsin, illustrates a typical example of the variation.

In many cases the relative variation in seedlings was largest under the treatment critical to growth or close to this. In other words, the responses of the individuals within a sample were not so uniform under the critical daylengths as under those daylengths that either allowed fast growth or were greatly inhibitory.

TABLE 10. Daylength¹ under which ratio of relative individual variation in the seedlings of the northern seed source to that of the southern source was greatest. Data for 8 species from the same greenhouse experiment as in Tables 7 and 8.

Species	Lat. of source	No. of seedlings ²	TREATMENT WITH MAXIMUM RATIO	
			in stem height	in top weight
Continental:				
<i>P. mariana</i>	61° 44°	17	LD	VLD
<i>P. banksiana</i>	60° 45°	15	VLD	VSD
<i>P. sylvestris</i>	60° 41°	14	LD	SD
<i>P. resinosa</i>	46° 42°	45	SD	SD
<i>P. rubens</i>	45° 42°	26	SD	SD
<i>P. rigida</i>	44° 35°	12	LD	SD
Maritime:				
<i>P. sitchensis</i>	60° 43°	21	LD	SD
<i>P. taxifolia</i>	50° 43°	17	VSD	VSD

¹ Daylength treatments described in Table 1.

² Number in each 5-in. pot.

RESPONSES TO EXTREME DAYLENGTHS

Since seed was available from the far north where midsummer day is extremely long, a special experiment was conducted under continuous illumination (ELD). The sunlight in the greenhouse was extended and supplemented with light from cool, white fluorescent tubes. The intensity of this at the plant level was about 300 f.c., which was somewhat less than un-

der the other treatments described in Table 1 (500 f.c.). However, the amount of the artificial light was somewhat higher because of the longer duration. The amount of the natural light, on the other hand was somewhat less. This experiment was arranged in the same way as the main experiments but only with 12 species and 21 seed sources.

In the far south the warm season is longer than the cold season and extends to the months when the days are shorter than 12 hours. To simulate these conditions, another special experiment (ESD) with various species was conducted. The sunlight in the greenhouse was supplemented with light from cool, white fluorescent tubes for 8 hours a day. The intensity of the artificial light was about 300 f.c. The material included the same species and seed sources as in the ELD experiment.

Because of the differences in the amounts of the light, these special treatments, especially ESD, were not strictly comparable with the other treatments. Nevertheless the different responses of various seed sources within each treatment were illuminating. It was obvious that the small amount of light in ESD was not too slight to permit normal growth for trees if these were not inhibited by the photoperiodic response. The amount of light in ELD was of the same magnitude as in the other treatments.

Continuous light (ELD), as compared to VLD, seemed to favor growth of most seed sources tested. Growth of northern seedlings was increased more than that of southern seedlings. For instance, seedlings of *A. negundo* from Saskatchewan (52°) and Montana (45°) grew at least as well as those from Louisiana (30°), although under other treatments they were clearly inferior (Fig. 5).

The far northern seedlings were especially favored by ELD. *P. mariana* from N.W.T. (61°), generally dormant even under VLD (Tables 5, 7), grew continuously and fast under ELD. Similarly, seedlings of *P. glauca* from Yukon (63°), mostly dormant under VLD, grew continuously under ELD reaching almost the same height (60 mm) as Wisconsin (46°) seedlings (66 mm). *B. papyrifera* from the far north elongated well under ELD though rosetted under other treatments. For instance, the seedlings from Northwest Territories grew about as tall (28 cm) as those (30 cm.) from Wisconsin.

The response of *P. sylvestris* from Finland (60°) was remarkable. The seeds from this source were much smaller than those from Spain (41°) and the growth rate was also much slower under the ordinary treatments (Table 7). Under ELD, however, the epicotyls of the seedlings from Finland were 66 mm long on the average as compared with 53 mm of those from Spain. This confirms an earlier finding (Vaartaja 1954) of the fast growth of northern *P. sylvestris* under continuous light.

Under the 8-hr photoperiod (ESD), the growth of most seedlings was conspicuously retarded resulting in dwarfing as shown in Fig. 5. Even most of those seed sources that were not clearly inhibited by

VSD, were obviously retarded by ESD. For instance, *P. sitchensis* from Oregon soon went into deep dormancy under ESD. Such southern seedlings as *P. strobus* from North Carolina (35°) and *A. negundo* from Louisiana (30°) were greatly inhibited. However, these did not seem to be affected quite so much as the northern seedlings of each species.

In a few species (*S. sempervirens*, *P. radiata*, *C. equisetifolia*) the inhibition by ESD was small and less certain. It may be significant that these represent the only seed sources from the maritime south or extremely low latitudes amongst those tested.

Thuja occidentalis grew very slowly under ESD. All three sources (44°, 45°, 50°) tested were inhibited. This is in accordance with the results of Phillips (1941) who found that this species was inhibited during winter in the greenhouse in Indiana. However, this species, as well as *T. plicata*, was an exception amongst northern types as it was not clearly affected by VSD.

The main results under ELD and ESD showed that the critical daylength was very long for far northern sources and extremely short for far southern sources. The results thus are essentially the same as those obtained with the main treatments.

DISCUSSION

INTERPRETATION OF THE RESULTS

The interaction of photoperiod and seed source was tested, as shown above by comparing the differences in each source under different daylength treatments.

The differences in terminal elongation were studied as far as expressed in early bud formation. The results (Tables 3 to 6) showed that in seedlings from most northern sources early dormancy occurred under longer daylengths than in seedlings from southern sources. The daylengths critical for the elongation of the northern sources are listed in Table 11.

The differences in other growth responses were expressed as the ratios $\frac{N}{S}$ ($= \frac{\text{northern source}}{\text{southern source}}$), in

the manner illustrated in the section "Examples." Most of these growth ratios were sharply reduced under certain daylengths inhibitory to northern sources (Fig. 1 to 5; Tables 7 to 9). These critical daylengths are listed in Table 11 for 18 comparisons. The probability levels for the interaction are also given in Table 11 for each species (except for the three species that were not subjected to statistical analysis).

The interaction means that the ratio of a seed source pair was different from one daylength treatment to another. Furthermore, it means that a likely genetic difference, which usually was expressed in a difference between two sources in one treatment, was not the same when observed in another treatment. In other words, an interaction indicated that photoperiodic responses were genetically different in latitudinally distant seed source populations. Such in-

TABLE 11. Daylengths critical for growth of northern ecotypes as compared with southern ecotypes. Summary of results in Tables 3 to 9.

Species	Lat. of source	DAYLENGTH ¹ AND P LEVEL ²			
		Buds ³ present	Depression in N/S ratio for		
			height	top weight	laterals
Continental:					
<i>B. papyrifera</i>	69° 42°	—	(VLD)	SD***	SD
<i>P. mariana</i>	61° 44°	VLD	VLD***	(VLD)**	(VLD)
<i>P. glauca</i>	60° 53°	LD	LD***	LD***	(LD)
<i>P. banksiana</i>	60° 45°	VLD	LD*	(LD)	SD*
<i>P. sylvestris</i>	60° 41°	VLD	LD*	LD*	(LD)
<i>P. abies</i>	57° 50°	LD	(LD)	—	—
<i>L. laricina</i>	54° 46°	SD	SD***	SD*	(SD)
<i>P. mariana</i>	52° 42°	LD	LD**	LD**	LD**
<i>P. pennsylvanica</i> var.					
<i>subintegerrima</i>	52° 33°	SD	(LD)	—	—
<i>A. negundo</i>	52° 45°	VSD	LD***	SD***	LD*
<i>U. americana</i>	51° 41°	LD	SD*	SD*	—
<i>P. strobus</i>	49° 35°	SD	(SD)	—	—
<i>P. resinosa</i>	46° 42°	all	(SD)	none	—
<i>P. rubens</i>	45° 39°	SD	(SD)	SD*	LD*
<i>P. rigida</i>	44° 35°	SD	VSD*	VSD*	LD*
Maritime:					
<i>P. sitchensis</i>	60° 43°	SD	SD***	SD***	LD*
<i>T. plicata</i>	58° 46°	—	(VSD)	VSD?*	VLD?*
<i>P. taxifolia</i>	50° 43°	VSD	VSD**	VSD**	—

¹ Daylength treatments; see Table 1.

² *** 0.01; ** 0.05; * 0.3 (probability levels for the maximum difference of the ratios of each species).

³ The longest day under which the majority of the northern seedlings had terminal buds at the age of 11 or 15 weeks; for *L. laricina* the buds appeared for the Wisconsin seedlings under the same daylength as for those from Manitoba; for N.W.T. seedlings the buds appeared under LD.

— = not studied

() = inconclusive results

? = doubtful results

teractions were found for most of the 17 species tested.

The decrease of the $\frac{N}{S}$ ratio observed under a critical daylength is explained as a result of the treatment-induced inhibition in the northern ecotype which is adapted to the relatively long days in high latitudes. The high ratio under VSD in some cases is explained as a result of both ecotypes being inhibited by such a short day.

Another finding that agrees with the hypothesis of photoperiodic ecotypes is the general correlation of the critical daylength and the latitude of seed source. The farther north the source, the longer was the longest day that inhibited growth. This can be seen in intraspecific comparisons of seed sources (Fig. 1; Table 3; *P. mariana* in Tables 5, 7, 8, 11), in interspecific comparisons of closely related species (Table 5) and in approximate intergeneric comparisons (Tables 2, 11).

The critical daylengths were shorter for two maritime species (*P. sitchensis* and *P. taxifolia*) than for the continental ones (Tables 5, 6, 11). This is as expected because under the oceanic influence the frost-free season lasts later in the season until daylength

is relatively short. On the other hand, in the continental climate there may be occasional early frosts when the daylength still is long. A dormant hardy condition may also be required because of a danger of summer drought in dry continental climates. The same correlation as within the continental group appears to hold within the maritime group (Tables 5, 6, 11), if the nonresponsive *T. plicata* is ignored.

As discussed further in the following section, photoperiodic ecotypes of trees may be considered as evolutionary adaptations to climate. Since climatic factors change gradually from one location to another, there may also be gradations between different photoperiodic responses. The populations in neighboring areas may occasionally exchange genes, and the population in any area may contain a mixture of slightly different photoperiodic biotypes. This explains the variation pattern found, such as in Fig. 1 and in Table 10. Under very favorable daylengths all the biotypes of the sample population grew well and the individual variation was normal; under the critical daylength certain biotypes were inhibited while others were not, which resulted in large variations; still shorter days did not allow any prolonged growth and the variation was small again.

The growth of certain species and genera showed their peculiar characteristics even though influenced by photoperiods and seed sources. For instance, the endogenous growth pattern was only modified by the treatments in *Pinus* while it was entirely overruled in *Picea*. This may have contributed to the result that no obvious interaction could be established for *Pinus resinosa*. The latitudinal distance of the sources compared was smaller for this species (4°) than for others, and hence the expected small interaction may have been too small to be established in the design with other species. In comparisons between very distant sources, e.g., *B. papyrifera* (latitudinal distance 27°), *Picea mariana* (17°), and *Picea sitchensis* (17°), the interactions were large and obvious. With *Pinus sylvestris* (19°), the statistical analyses gave less convincing interactions for each single response. However, because the pattern in the data and all the different types of data agreed with the hypothesis, as did also the data from another separate experiment, the interactions recorded for this species should be real. Similarly, the same pattern and agreement of various data were found with all other species tested, except *P. resinosa* and *T. plicata*.

Growth pattern and dormancy of trees is obviously affected by an endogenous rhythm. Each tree species follows a certain pattern in its seasonal growth (Kramer 1943, 1957, Kozłowski & Ward 1957a, 1957b), and seasonal earliness is peculiar even to tree individuals (Morris *et al.* 1957, McMillan 1957b). The growth period tends to be shorter in northern trees than in southern trees. This tendency was shown in the earliness of terminal dormancy of northern trees in certain data in Tables 3 to 5. The question arises as to the relationship of photoperiodic ecotypes and endogenously different growth patterns.

The photoperiodic ecotype is a population that has, during evolution, adapted to its seasonally changing environment through a photoperiodic stimulus in a way different from the adaptation elsewhere in other populations. This ecological definition does not make any assumptions in regard to the mechanisms in the adaptation. Any important function in the tree that is affected by photoperiods may take part in the adaptation. The foregoing data, with the possible exception of *P. resinosa* and *T. plicata*, showed that the endogenous growth pattern was either modified or entirely obscured by the effects of photoperiod. Until the physiological processes that operate in photoperiodic responses and in the adaptation mechanisms are known, the hypothesis of photoperiodic ecotypes must remain descriptive rather than causative. It gives meaning and order for observed facts but does not explain the chain of the actual causes. Similarly, the theory of differences in growth pattern so far describes rather than explains certain adaptive growth phenomena. Because of this situation, no more speculation is given of the possible role of endogenous rhythm in photoperiodic ecotypes.

This study suggests that at least 15 species out of 17 tested in 8 out of 9 genera (*Acer*, *Betula*, *Fraxinus*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, and *Ulmus*) contain photoperiodic ecotypes. In addition to *Populus*, which also appears to contain photoperiodic ecotypes (Pauley & Perry 1954), and *Quercus* which has not yet been studied, these genera represent the most important and widespread trees north of the tropics. Thus, photoperiodic ecotypes seem to exist commonly in trees, at least in those with wide north-south range in the northern hemisphere.

The results of this study are in accordance with the earlier evidence of photoperiodic ecotypes as discussed in "Introduction." The results extend the evidence to more species and, for species studied earlier, confirm the evidence which, with the possible exception of data by Pauley & Perry (1954) and Vaartaja (1954), was somewhat disputable. The earlier evidence of nonexistence of photoperiodic ecotypes may be valid for the particular species but needs to be confirmed because this evidence dealt with relatively southern ecotypes and rather limited latitudinal ranges. In these, the photoperiodic response is expected to be small (Table 2) and hence the possible differences between ecotypes probably are very small and difficult to demonstrate.

FUNCTION OF THE PHOTOPERIODIC ECOTYPE

Why should northern trees possess their peculiar photoperiodic response? Under the optimal experimental conditions in a greenhouse the response only handicapped the trees. In nature, the dormancy response obviously serves to adapt the tree to some other factors associated with short days. These could be the advent of the cold season, or perhaps seasons with early frosts or droughts, or all of these, combined.

One would expect an adaptation mechanism to cold to be actuated by temperature. This expectation is a result of the habit of separating the environment

into factors, and of focusing attention on those phenomena which exhibit simple orderliness and purpose in nature. However, according to prevalent theories, the raw material for evolution is rather random, purposeless variation. Accordingly, the adaptation mechanism could have evolved from the response of the plant to photoperiods, just as well as from a direct response to temperature itself, once such a response increased the fitness of the plant and thus was favored by selection. In fact, the indirect way increases the fitness of a tree more than a direct one could do. It gives to the trees a safety margin which makes them more independent of factors that change irregularly. During the peculiarly long life of trees, rainy or warm seasons would tend to lead the evolution in a dangerous direction if the natural selection were based only on direct effects, and a sudden cold or drought could be catastrophic. Direct mechanism could not prepare the tree to meet sudden unfavorable weather changes beforehand as does the indirect mechanism based on daylength.

It is especially difficult to explain by any immediate effects the importance of the cessation of elongation in certain trees long before the cold season begins, as in species of *Pinus*. If the cessation is considered as an adaptation to occasional desiccation of soil in mid-summer, it is easy to understand. This would be especially important for many species of *Pinus* that usually occupy dry sites.

Rapid flush of elongation during the least dangerous time would also increase the fitness of trees on sites that are subject occasionally to early frosts. In such trees the control of elongation may be quite independent from that of other growth. After the elongation phase, which is most vulnerable to cold and drought, other types of growth still take place until the risks of the season are too severe for growth activity of any kind. This was suggested particularly by the results with *Betula papyrifera* from the far north. Photoperiods that inhibited elongation, permitted great increases in weight of stem and roots, and in numbers of buds. Similarly, Wareing (1956) and Wareing & Roberts (1956) found that the terminal growth was inhibited by a shorter day than was the cambial growth in *Pinus sylvestris* and *Robinia pseudoacacia* L. Further studies are needed to determine the detailed sequence of various growth types in different ecotypes and its dependence on photoperiods.

The physiological basis of photoperiodism may be in pigment reactions common in many plants and governing various responses (Borthwick *et al.* 1956). However, it is not yet explained how the mechanism would allow such gradual clinal differences in photoperiodic responses as appear to exist.

Temperature interacts with photoperiods in growth and dormancy phenomena in many tree species. Kramer (1957) suggested that thermoperiodism or effects of diurnal temperature cycle, is more important than photoperiodism in the growth of *Pinus taeda*. Considering how all physiological processes are af-

ected by temperature, it would be surprising if most growth activities would not be retarded by low temperatures. Downs & Borthwick (1956) found that temperature varying between 60 and 70° F. strongly suppressed growth of many species. Grull & Wettstein (1955) found that the growth of altitudinal races of *P. sylvestris* appeared to vary under two photoperiods depending on the weather. Examples of the interaction of temperature and photoperiods on dormancy in trees are also given by Moshkov (1935), Olmsted (1951), and Irgens-Moller (1957). Vegis (1955) suggested that maximum temperature generally interacts with photoperiods. In his experiments with a water plant (*Hydrocharis*), bud formation was increased by the interaction of decreasing photoperiods and increasing temperatures. He even suggested that the primary difference between the northern and southern ecotypes of trees would be in their different critical maximum temperature.

Because the photoperiodic ecotype likely has evolved and functions mainly as an indirect mechanism for adapting the plant to various seasonal changes and to factors other than the photoperiod itself, these ecotypes were not always found and should not be expected to be exactly similar in each latitude. The critical daylength of high altitude ecotypes should be longer than that of other ecotypes because of the short warm season in mid-summer only. The studies of Karschon (1949) and Pauley & Perry (1954) suggested that this indeed is the case. Analogously the critical daylength should be longer for continental trees than for maritime trees. This appears to be the case, at least in interspecific comparisons of the present study.

The severity of winter and length of warm season of course are usually in close correlation with latitudes and hence with photoperiods except in mountainous areas. In this paper, only latitudinally distant seed source pairs were compared. This crude method was used to test existence of photoperiodic ecotypes in many species. In future studies the seed sources of each species should be more numerous and they should be spaced more closely and extended in longitudinal and vertical directions. Because of the dynamic nature of evolution, the distribution of tree ecotypes may be correlated even with migratory factors. An extensive study on seed sources of *Acer saccharum* (Kriebel 1957) suggested that the influence of the evolutionary trends due to glaciation is still recognizable in the distribution of ecotypes of this species in the Appalachians.

Plant species are known to contain various types of climatic ecotypes (Turesson 1922a, 1922b, 1930, Clausen *et al.* 1948, Clausen 1951, McMillan 1957a and b), edaphic ecotypes (Turesson 1922a and b, 1929, Gregor 1946, Kruckeberg 1951), and biotic ecotypes (Tadros 1957). It has also been shown that these vary in different directions and are superimposed upon each other. This makes it difficult to recognize photoperiodic ecotypes morphologically, especially when the variation is gradual. Yet the differences

can be quite conspicuous if produced by proper experiment. This is true at least when distant samples are compared, as in the present study. The ecotype variation demonstrated in this study may be discontinuous due to more or less definable ecotypes or, more often, continuous, due to such ecoclines as described and discussed by Huxley (1938), Gregor (1944, 1946), and Stebbins (1950).

The data of this study (Fig. 1, Table 10) suggested that each seed source population contained biotypes with some variation in their photoperiodic responses. This could be seen most clearly under a certain critical daylength. The same phenomenon may be expressed in the conspicuous differences in tree individuals in nature when observed at the times of leafing, fall colouring, or leaf abscission. This is especially pronounced in poplar stands because many poplar species usually, or always in certain areas (Cottam 1954), reproduce vegetatively and form distinct groups of genetically alike individuals.

Ecotypes, photoperiodic ecotypes included, are not only important means of the species in their adaptation to environment but are tools of evolution also in another manner. Ecotypic differences may increase genetic barriers within species and thus initiate evolution of new species (Stebbins 1950, Clausen 1951). Photoperiodic ecotypes might exhibit differences in seasonal development, including the time of flowering, and hence cause restrictions in hybridization.

PRACTICAL IMPORTANCE OF PHOTOPERIODIC ECOTYPES

The unfortunate experience of foresters in Europe has led to this advice: do not plant tree seeds or seedlings far away from their point of origin. Violation of this rule has caused great economic losses so that laws have been passed to prevent it. Foresters started to study this problem by planting different "tree provenances" in the same plantation. Differences were observed quite early in spite of the fallacy persistent in the last century that most individuals of a species were genetically alike (Schott 1904, Schotte 1904, Engler 1905, Ciesler 1907, further references in Langlet 1936, Kalela 1938, Sylven 1940). The provenance trials have served mainly the practical purpose of finding seed sources safe to plant in a locality. Some broadly general rules have also emerged. For instance, in the uniform climate of Finland, tree seed can be transferred successfully in east-west directions (Heikinheimo 1949). If seed is transferred southwards, the seedlings will grow slowly although survival may be high. If seed is transferred a little northwards, the seedlings often outgrow the native seedlings. This can be done only within limits of a few hundred kilometers; otherwise the seedlings would die from early frosts or winter damage. In mountainous Sweden it is also necessary to consider the elevation which limits seed transfers in east-west directions.

The basic causes for the importance of seed source are now easy to understand. By means of extensive provenance trials (or "uniform garden technique"),

Turesson (1922a, 1922b, 1929, 1930) discovered that many plant species consist of genetically different populations, each being adapted to its own peculiar environment. Ecotypic variation was found on sites which differ in edaphic or climatic respects, especially in certain species with wide geographic range. Evidence of this has been steadily increasing also for trees. Langlet (1936, 1943) studied 582 seed lots of *Pinus sylvestris* from various sources, mainly in Sweden. When the seedlings were grown in a nursery in central Sweden, the dry substance and sugar content in needles during late fall were clearly correlated with latitude of the source. Langlet considered these properties of the seedlings as heritable adaptations to the climate (1936), and possibly to photoperiods (1943). There was also correlation with the length of the warm season at the seed source; analysis suggested that this factor could cause nearly $\frac{2}{5}$, and the latitude $\frac{3}{5}$, of the variation. In a provenance trial of 43 *Acer saccharum* sources, Kriebel (1957) found several interesting correlations. Susceptibility to heat injury, time of leafing in spring, time of terminal dormancy, and time of leaf coloration were correlated with latitude and temperature at the seed source. The single factor most highly correlated was latitude, suggesting the possible importance of photoperiodism. Similarly, Stoeckeler & Rudolph (1956) found that growth and winter color of *Pinus banksiana* seedlings were clearly correlated with latitude of seed source in a test involving 29 sources.

The provenance technique is valuable for distinguishing between variations in trees that are controlled genetically and those controlled by environment. It should be emphasized, however, that the results obtained in one provenance trial, even when based on extensive data, often can not be applied to another environment. Such common generalizations as "a certain tree race is hardy, or early, or slow growing," are meaningless. It is necessary to specify also to what environments such statements apply. This is demonstrated by the results of the present study. The growth of a certain provenance which was slow under certain photoperiods was often fast under others. The results provided excellent examples of biological phenomena where both genetic and environmental factors are very important and neither can be considered alone. This is demonstrated, for instance, in Fig. 1. The seedlings of each seed source were quite different under different environments, except in one case. The seedlings from latitude 46°, as a contrast to those from 60°, were not markedly affected by the environmental difference between LD and VLD. The genetic differences, as represented by the difference between northern and southern population samples, caused large differences in phenotypes under three of the environments, but not under VLD.

To obtain a reasonable idea of the potentiality of a tree race, it is necessary to compare it with other races in several environments. This would require more extensive provenance trials with increased coordination through international cooperation. A start in this

direction has been made with *Pinus sylvestris* and *Picea abies* (Heikinheimo 1954).

Interpretation of the provenance data will be easier when the responses of various provenances to single factors and to their interactions are known. It may become possible to establish generally valid rules to follow instead of the present situation where the potentialities of a tree ecotype must be empirically tested for each locality. It may become possible to avoid much of the frustration that so far has accompanied the efforts to grow exotic trees.

The desired responses to various factors can be achieved through breeding. This may greatly extend the use of exotic tree species and their specific properties. To utilize this possibility to the full extent requires better knowledge of the responses of trees to various factors.

The results of the present study suggest that the photoperiodic responses and differences in these are of basic importance to growth, development, and morphology of many trees. Smatok (1956) found that the carbohydrate content was increased in leaves of *Syringa* and *Caragana*, and decreased in roots, with increasing photoperiods. This suggests that much of the physiological work already done on trees may need to be repeated with consideration to all the possible profound effects of photoperiods.

The results of this study suggest that it may not be safe to transfer trees even to a site where the thermoclimate is the same as at their origin without considering also the photoclimate. This is because the photoperiodic response of trees appears to be an indirect mechanism in their climatic adaptation. For instance, there may be areas in Canada and Siberia, or in southern mountains and northern lowlands where the climates are the same but latitudes and photoperiods differ. At the more northern site the day would still be long at the time of season when the climate would require dormancy. When trees adapted to this situation are transferred south where days are shorter, the new environment would cause early dormancy although temperature would still be favorable for growth. The common undue earliness of the onset of dormancy and slow growth of northern trees in provenance trials may be largely due to this kind of situation.

A converse situation occurs when trees are transferred far into more northern latitudes. The trees freeze because at their original site they have become adapted to be in full growth under the fairly long photoperiods that prevail when winter cold or early frosts start at the new site. Overwintering can be improved by artificially shortening the photoperiod (Moshkov 1935, Davidson & Hamner 1957, Robak 1957).

To illustrate photoperiodic reactions of trees under outside conditions, data taken from the international provenance trials (as reported by Heikinheimo 1954) are analyzed in Table 12. The first part of the table gives weights of *P. abies* seedlings as slightly simplified from the published data. The growth of

provenance in one nursery should not be compared with that in another nursery because of differences in soil fertility, weather, length of frost-free season, and other factors. On the other hand the different responses of different provenances grown in each of the nurseries are illuminating.

TABLE 12. Weight of seedlings of *Picea abies* from different seed sources when grown at distant nurseries for one year. Data of Heikinheimo 1954. Calculations of O. Vaartaja.

Source	Lat.	FRESH WEIGHT (GM) WHEN GROWN IN				
		66°	60°	55°	51°	47°
Finland.....	66°	n 8	5	5	3	2
Finland.....	62°	s ↓ 11	9	12	8	4
Norway.....	60°	8	n 14	10	9	4
Latvia.....	57°	12	s ↓ 20	n 18	14	10
Germany.....	52°	15	21	s ↓ 32	n 26	14
Czechoslovakia.....	49°	14	29	35	s ↓ 28	13
Switzerland.....	48°	11	23	36	29	16
Germany.....	47°	14	28	30	30	n 14
Italy.....	46°	17	22	31	29	s ↓ 11
France.....	45°	15	18	23	29	13
Bulgaria.....	42°	13	17	38	27	10
Northern (n) group		Mean, gm 8	9	11	12	10
		Range, gm —	9	13	23	14
		Range, % —	100	118	180	140
Southern (s) group		Mean, gm 13	22	32	29	11
		Range, gm 9	12	15	3	3
		Range, % 69	55	47	11	9

n=sources north from or at the test site.
s=sources south from the test site.

It is expected that response to abnormally long photoperiod is small and to abnormally short photoperiod large (e.g., Fig. 5). Therefore, the weight data were divided into two parts in Table 12: in each column (nursery) the seed sources originating north (n) of the nursery, or at it, were separated with a line from the more southerly (s) sources. The range (difference between the highest and lowest weight value) was calculated for each part and shown in the bottom of the table. As expected, there was a large range (100 to 180%) in seedlings (n), transferred to photoperiods shorter than at their origins; there was only a small range (9 to 69%) in the seedlings (s) transferred to longer photoperiods. Furthermore, the variation in group (s) was irregular while in (n) it was very regularly correlated with the latitude of source. This shows excellent agreement between actual response of the seedlings and of the response expected according to the theory of photoperiodic eco-

types. The data thus suggest that photoperiodic ecotypes operate and have actual importance not only in experiments but also under natural climatic conditions.

After some allowance was given to the effects of seed size and stand density, the data (from Heikinheimo 1954) on *P. sylvestris* showed trends similar to those of *P. abies*. Conclusions in accordance with the hypothesis could also be made on data of the long-term survival of both these species. Seedlings far north from their origin gradually died, apparently as a result of being insufficiently hardened under the long autumn photoperiods in the north.

The fact that trees can be advantageously transferred northwards within certain limits is a result of two circumstances: (a) the "safety margin" by which trees have become adapted to thermoclimate, and (b) the recent trends towards increasing temperatures during about the past 50 yrs (Lysgaard 1950, Willet 1950). Utilizing the latter involves a serious risk. Long-living trees should not generally be transferred northwards even after successful short term trials unless climatologists can give reasonable assurance that the trend will continue. However, the risk may be less for species that are still in a natural process of slowly migrating northwards since the glaciation (e.g., clonally spreading aspen?) than for species that have already become balanced with their environment.

When trees are grown south of their site of origin, they may enter into dormancy that is abnormally early and deep. This results in hardness and slow, compact growth habit. This may explain the fact, for instance, that *P. abies* from high latitudes in Scandinavia, where it is sensitive to drought, survives well in the more southerly but extreme climate in the American prairies. The slow compact growth is sometimes desirable also for ornamental purposes.

SUMMARY

The hypothesis of photoperiodic ecotypes was tested with 38 tree species of 19 genera and 81 seed sources from various latitudes in the northern hemisphere. The 4 greenhouse test conditions differed photoperiodically but received the same amount of light from sun and fluorescent tubes. In general, the farther north the seed source, the greater was the response to test conditions, and the longer was the maximum ("critical") daylength that strongly inhibited the seedlings. The interaction of seed source and photoperiod was analyzed in comparisons of latitudinally distant seed source pairs within 17 species belonging to 9 genera. In most cases interactions were recorded in the following responses: (1) Duration of elongation. Under certain daylengths elongation of northern seedlings soon ceased while it continued in southern seedlings. No difference or less was found under other daylengths. The endogenous seasonal elongation pattern was entirely overruled by the effects of photoperiods in many species (e.g., 5 *Picea* spp.) or only modified in others (e.g., 5 *Pinus* spp.). (2) Amount of growth. Height and top weight of

northern as compared to southern seedlings were very small under certain daylengths but not under others. The growth responses followed a certain pattern in accordance with the hypothesis. (3) Lateral development. Number of side branches and buds was restricted in northern seedlings under short days. All these facts are in accordance with the hypothesis. Individual variation was usually greatest at the critical daylength, as would be expected if the populations were somewhat mixed in their inherited responses to photoperiods.

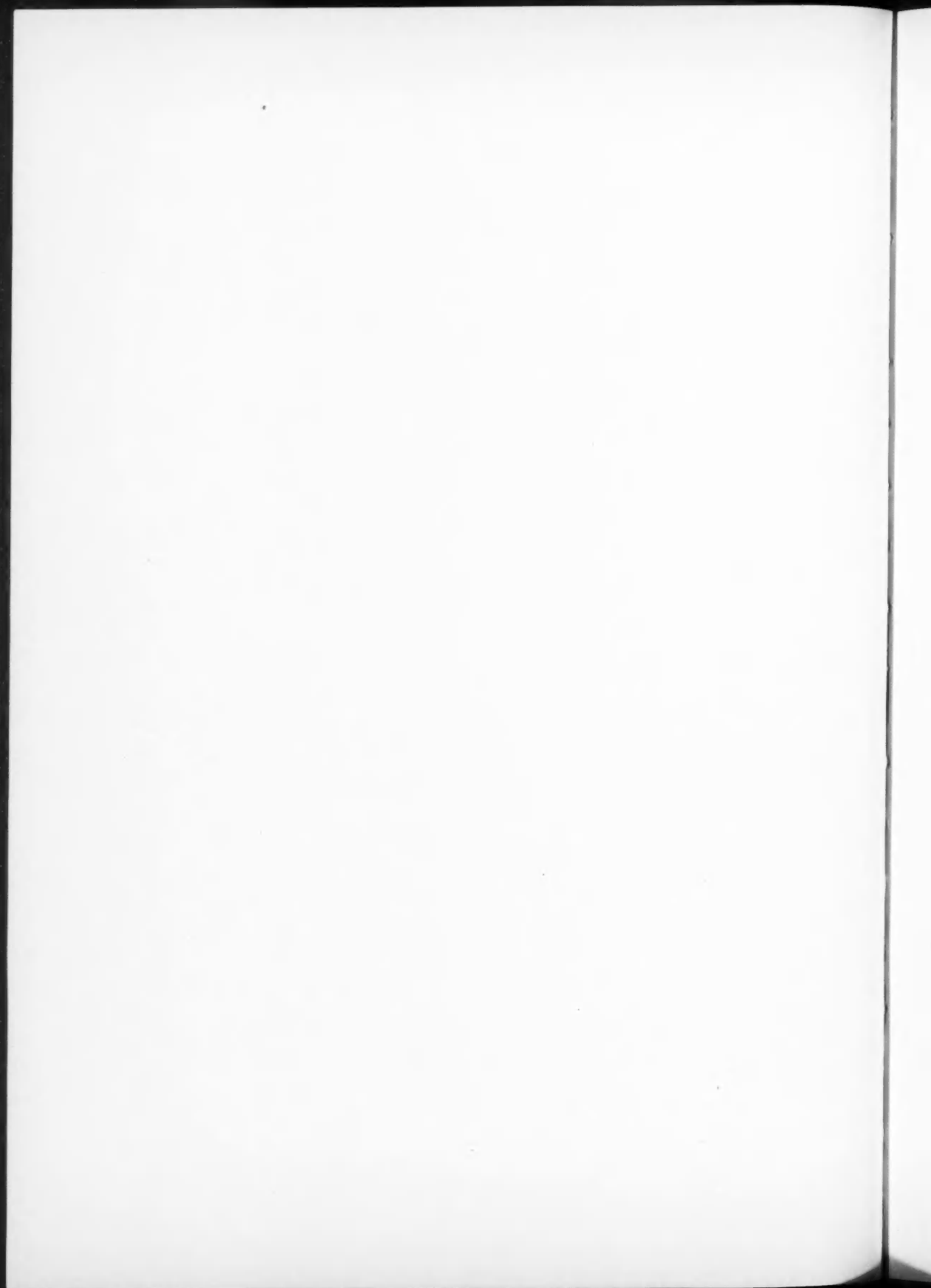
It is suggested that the photoperiodic ecotypes have evolved as an indirect mechanism in the adaptation of trees to various seasonally changing climatic factors. Therefore, they are only approximately similar at different sites in each latitude.

LITERATURE CITED

- Allard, H. A. & M. W. Evans. 1941. Growth and flowering of some tame and wild grasses in response to different photoperiods. *Jour. Agr. Res.* 62: 193-228.
- Alleweldt, G. 1957. Der Einfluss von Photoperiode und Temperatur auf Wachstum und Entwicklung von Holzpflanzen unter besonderer Berücksichtigung der Gattung *Vitis*. *Vitis* 1: 159-180.
- Balut, S. 1956. Der Einfluss der Tageslänge und der Temperatur auf den Verlauf des einjährigen Lebenszyklus der Samlinge *Fagus silvatica* L. und *Abies alba* Mill. (Polish with German summary.) *Ekol. Polska*, Ser. A. 4: 225-292.
- Borthwick, H. A., S. B. Hendricks, & M. W. Parker. 1956. Photoperiodism. In *Radiation Biology* 3: 479-517. New York: McGraw-Hill Book Co., Inc.
- Cieslar, A. 1907. Die Bedeutung klimatischer Varietäten unserer Holzarten für den Waldbau. *Centralbl. f. das Gesam. Forstw.* 33: 1-19.
- Clausen, J. 1951. Stages in the evolution of plant species. Ithaca, New York: Cornell University Press.
- Clausen, J., D. D. Keck & W. M. Hiesey. 1948. Experimental studies on the nature of species. III. Environmental responses of climatic races of *Achillea*. *Carnegie Inst. Wash. Publ.* 581.
- Cottam, W. P. 1954. Prevernal leafing of aspen in Utah mountains. *Arnold Arboretum Jour.* 35: 239-248.
- Critchfield, W. B. 1957. Geographic variation in *Pinus contorta*. Maria Moors Cabot Foundation (Harvard Univ.) Publ. 3.
- Davidson, H. & C. L. Hamner. 1957. Photoperiodic responses of selected woody ornamental shrubs. *Mich. Agr. Expt. Sta. Quart. Bull.* 40: 327-343.
- Downs, R. J. & H. A. Borthwick. 1956. Effects of photoperiod on growth of trees. *Bot. Gaz.* 117: 310-326.
- Eckert, W. J. & G. M. Clemence. 1946. Tables of sunrise, sunset, and twilight. U. S. Naval Observatory, Washington.
- Engler, A. 1905. Einfluss der Provenienz des Samens auf die Eigenschaften der forstlichen Holzgewächse. *Schweiz. Centralanst. f. Forstl. Versuchsw. Mitt.* 8: 81-236.
- Garner, W. W. & H. A. Allard. 1923. Further studies in photoperiodism, the response of the plant to rela-

- tive length of day and night. Jour. Agr. Res. 23: 871-885.
- Gregor, J. W. 1944. The ecotype. Biol. Rev. 19: 20-30.
- . 1946. Ecotypic differentiation. New Phytol. 45: 254-270.
- Grehn, J. 1952. Über Spaltungserscheinungen und photoperiodische Einflüsse bei Kreuzungen innerhalb der Sektion Leuke Duby. Ztschr. Forstgenetik Forstpflanzenz. 1: 61-69.
- Grull, H. & W. Wettstein. 1955. Photo- und thermoperiodische Einflüsse auf das Wachstum der Kiefer (*Pinus silvestris*). Holzforschung 9: 81-84.
- Heikinheimo, O. 1949. Tuloksia kuusen ja mannyn maantieteellisillä rodulla suoritetuista kokeista. Results of experiments on the geographical races of spruce and pine. Inst. Forest Fenniae Commun. 37: 1.
- . 1954. Taimitarkan maantieteellinen sijainti, siemenen alkuperä ja istutuskaudet. Geographische Lage der Baumschule, Herkunft des Samens und Zeit der Pflanzung. Acta Forest. Fenn. 61: 9.
- Hoffman, D. 1953. Die Rolle des Photoperiodismus in der Forstpflanzenzüchtung. Ztschr. Forstgenetik Forstpflanzenz. 2: 44-47.
- Huxley, J. S. 1938. Clines, an auxiliary taxonomic principle. Nature 142: 219.
- Irgens-Møller, H. 1957. Ecotypic response to temperature and photoperiod in Douglas-fir. Forest Sci. 3: 79-83.
- Johnsson, H. 1956. Heterosiserscheinungen bei den Hybriden zwischen Breitengradsrassen von *Populus tremula*. Ztschr. Forstgenetik Forstpflanzenz. 5/6: 156-160.
- Kalela, A. 1938. Zur Synthese der experimentellen Untersuchungen über Klimarassen der Holzarten. Inst. Forest Fenniae Commun. 26: 1.
- Karschön, R. 1949. Untersuchungen über die physiologische Variabilität von Föhrenkeimlingen autochthoner Populationen. Schweiz. Anstalt forstl. Versuchsw. Mitt. 26: 205-244.
- Kozłowski, T. T. & R. C. Ward. 1957a. Seasonal height growth of conifers. Forest Sci. 3: 61-66.
- Kozłowski, T. T. & R. C. Ward. 1957b. Seasonal height growth of deciduous trees. Forest Sci. 3: 168-174.
- Kramer, P. J. 1943. Amount and duration of growth of various species of tree seedlings. Plant Physiol. 18: 239-251.
- . 1957. Some effects of various combinations of day and night temperatures and photoperiod on the height growth of loblolly pine seedlings. Forest Sci. 3: 45-55.
- Kriebel, H. B. 1957. Patterns of genetic variation in sugar maple. Ohio Agr. Expt. Sta. Res. Bull. 791.
- Kruckeberg, A. R. 1951. Intraspecific variability in the response of certain native species to serpentine soil. Amer. Jour. Bot. 38: 408-419.
- Langlet, O. 1936. Studier over tallens fysiologiska variabilitet och dess samband med klimatet. Ett bidrag till kannedomen om tallens ekotyper. Studien über die physiologische Variabilität der Kiefer und deren Zusammenhang mit dem Klima. Beiträge zur Kenntniss der Ökotypen von *Pinus silvestris* L. Medd. Skogsforsöksanst. 29: 219-470.
- . 1943. Photoperiodismus und Provenienz bei der gemeinen Kiefer (*Pinus silvestris* L.) Medd. Skogsforsöksanst. 33: 298-330.
- Larsen, E. C. 1947. Photoperiodic responses of geographical strains of *Andropogon scoparius*. Bot. Gaz. 109: 132-149.
- Lawrence, W. J. C. 1955. Glasshouse design and management. Hort. Soc. Jour. 80: 358-365.
- Lysgaard, L. 1950. On the present climatic variation. Roy. Meteor. Soc. Cent. Proc. 206-211.
- McMillan, C. 1957a. Nature of plant community. III. Flowering behavior within two grassland communities under reciprocal transplanting. Amer. Jour. Bot. 44: 144-153.
- . 1957b. Nature of plant community. IV. Phenological variation within five woodland communities under controlled temperatures. Amer. Jour. Bot. 44: 154-163.
- Morris, W. G., R. R. Silen & H. Irgens-Møller. 1957. Consistency of bud bursting in Douglas-fir. Jour. Forestry 55: 208-210.
- Moshkov, B. S. 1935. Photoperiodismus und Frosthärte ausdauernder Gewächse. Planta 23: 774-803.
- Nitsch, J. P. 1957. Growth responses of woody plants to photoperiodic stimuli. Amer. Soc. Hort. Proc. 70: 512-525.
- Olmsted, C. E. 1944. Growth and development in range grasses. IV. Photoperiodic responses in twelve strains of side-oats grama. Bot. Gaz. 106: 46-74.
- . 1951. Experiments on photoperiodism, dormancy, and leaf age and abscission in sugar maple. Bot. Gaz. 112: 365-393.
- Olson, J. S. & H. Nienstaedt. 1957. Photoperiod and chilling control growth of hemlock. Science 125: 492-494.
- Pauley, S. S. 1950. Forest-tree breeding work of the Cabot Foundation. Arnoldia 10: 1-8.
- Pauley, S. S. & T. O. Perry. 1954. Ecotypic variation of the photoperiodic response in *Populus*. Arnold Arboretum Jour. 35: 167-188.
- Perry, T. O. & W. C. Wu. 1957. Cooperative forest genetics research program. Fla. Univ. School of Forestry. Res. Rept. 4: 21-22.
- Phillips, J. E. 1941. Effect of day length on dormancy in tree seedlings. Jour. Forestry 39: 55-59.
- Robak, H. 1957. Sambandet mellom daglengden og avslutningen av den arlige vekstperioden hos en del naletreslag av interesse for vart skogbruk. Orienterende undersøkelser i Ekhaug forsøkshage på Syfteland. On the connection between day length and termination of the annual growth period in seedlings of some conifers of interest to Norwegian forestry. Preparatory experiments made at Ekhaug Experimental Nursery near Bergen, Norway. Vestlandets Forstl. Forsøkssta. Meddel. 31.
- Schott, P. K. 1904. *Pinus sylvestris* L. Die gemeine Kiefer. Beiträge zur Systematik und Provenienzfrage mit besonderer Berücksichtigung des in Deutschland in den Handel kommenden Samens. Forstwiss. Centbl. 26.
- Schotte, G. 1904. Om betydelsen av skogsfroets geografiska härstamning. Svensk Skogsv.-foren. tidskr. Stockholm.
- Smatok, I. D. 1956. The effect of day length under polar conditions on the carbohydrate and mineral content of *Caragana arborescens* and *Syringa vulgaris*. (Russian) Akad. Nauk S.S.S.R. Dok. 111: 213-216. [Rev. 1025 in Hortie. Abs. 27: 170 (1957)].

- Stebbins, G. L., Jr.** 1950. Variation and evolution in plants. New York: Columbia Univ. Press.
- Stoeckeler, J. H. & P. O. Rudolf.** 1956. Winter coloration and growth of jack pine in the nursery as affected by seed source. *Ztschr. Forstgenetik Forstpflanz.* 5: 161-165.
- Sylvén, N.** 1940. Lang-och kortdagstyper av de svenska skogsträden. Long day and short day types of Swedish forest trees. *Svensk Papperstidn.* 43: 317-324; 332-342; 350-354.
- Tadros, T. M.** 1957. Evidence of the presence of an edapho-biotic factor in the problem of serpentine tolerance. *Ecology* 38: 284-307.
- Turesson, G.** 1922a. The species and the variety as ecological units. *Hereditas* 3: 100-113.
- . 1922b. The genotypical response of the plant species to the habitat. *Hereditas* 3: 211-350.
- . 1929. Zur Natur und Begrenzung der Arteneinheiten. *Hereditas* 9: 81-101.
- . 1930. The selective effect of climate upon the plant species. *Hereditas* 14: 99-152.
- Vaartaja, O.** 1954. Photoperiodic ecotypes of trees. *Canad. Jour. Bot.* 32: 392-399.
- . 1957a. Photoperiodic responses in seedlings of northern tree species. *Canad. Jour. Bot.* 35: 133-138.
- . 1957b. Experimental evidence of photoperiodic ecotypes in several tree species. *Ecol. Soc. Amer. Bull.* 38: 76.
- Vegis, A.** 1955. über den Einfluss der Temperatur und der täglichen Licht-Dunkel-Periode auf die Bildung der Ruheknospen zugleich ein Beitrag zur Entstehung des Ruhezustandes. *Symbolae Bot. Upsaliensis* 14: 1-175.
- Wareing, P. F.** 1948. Photoperiodism in woody species. *Forestry* 22: 211-221.
- . 1956. Photoperiodism in woody plants. *Ann. Rev. Plant Physiol.* 7: 191-214.
- Wareing, P. F. & D. L. Roberts.** 1956. Photoperiodic control of cambial activity in *Robinia pseudoacacia* L. *New Phytol.* 55: 356-366.
- Wassink, E. C. & J. H. Wiersma.** 1955. Daylength responses of some forest trees. *Acta Bot. Neerl.* 4: 657-670.
- Waxman, S.** 1956. The effect of the length of day on the growth of woody plants. *Plant Propagators Soc. Proc.* 5: 47-50.
- Wettstein, W. von.** 1942. Möglichkeiten der Züchtung neuer Ökotypen nach Kreuzung. *Züchter* 14: 282-285.
- Willet, H. C.** 1950. Temperature trends of the past century. *Roy. Meteor. Soc. Cent. Proc.* 195-206.
- Zelawski, W.** 1957. Further researches on the photoperiodic reaction in seedlings of the European larch (*Larix europaea* D. C.) (Polish with English summary). *Soc. Bot. Polon. Acta* 26: 79-103.



SPATIAL AND TEMPORAL MOVEMENTS OF A POPULATION OF THE PAINTED TURTLE, *CHRYSEMYS PICTA MARGINATA* (AGASSIZ)

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INTRODUCTION

There has been an increasing amount of information accumulating over the past two or three decades which deals with the territories, activity ranges, and home ranges of many animals, both vertebrate and invertebrate, aquatic and terrestrial. That this interest has been actively shared by investigators working with turtles is shown by the papers of Pearse (1923), Cagle (1944, 1950), Williams (1952) and Breckenridge (1955) on fresh water turtles, by those of Carr & Caldwell (1956) and Carr & Giovannoli (1957) on marine turtles, and by those of Breder (1927), Nichols (1939), Woodbury & Hardy (1948), and Stickle (1950) on terrestrial species. These investigations, as well as most others dealing with the spatial movements of assorted animals, were concerned with establishing whether or not the animals studied restricted their activities to limited areas or, if such areas were found to exist, with their size, shape, and permanence. The present investigation was undertaken with the following ends in view: (1) to verify or refute the general belief that the painted turtle, *Chrysemys picta*, restricts its movements to certain small areas, (2) to identify any physical or biological factor associated either with changes in the size and location of an activity range or with the spatial and temporal stabilization of those same areas, (3) to ascertain the seasonal variation in activities of a population of turtles over a period of several years.

A debt of gratitude is due Professor Frederick H. Test for his aid. Drs. Pierre Dansereau, Francis Evans, Norman Hartweg, Herbert Wagner and

Hampton Carson gave many valuable suggestions. The late Professor J. Speed Rogers and Professor T. H. Hubbell offered me the use of the Edwin S. George Reserve. The curator of the Reserve, Dr. Irving Cantrall, and the custodian, Mr. Lawrence Camburn, helped me considerably while I worked there. Dr. F. K. Sparrow and Miss L. Hillis kindly identified the plants. Mr. Laurence Joline drew some of the figures. Financial aid was provided by the National Science Foundation, the George Reserve Research Fund, and the Summer Research Fund of the Graduate School of Washington University. My wife, Mildred Bloomsburg Sexton, was a constant aid.

LOCATION AND DESCRIPTION OF THE AREA

The population of turtles most intensively studied inhabited five bodies of water on the Edwin S. George Reserve, located in Putnam Township, Livingston County, Michigan (Fig. 1). These five are Southwest Swamp, Fishhook Marsh, Crane Pond, the Ditch, and Cattail Marsh. During periods of great precipitation, late winter, spring, and sometimes during the fall, some water flows southward from Fishhook Marsh into Southwest Swamp, while the remainder flows eastward from the former into Crane Pond. As the flow continues into Crane Pond from Fishhook Marsh, the water level in the latter drops below that of Southwest Swamp so that the water from Southwest Swamp reverses its flow, passing back into Fishhook Marsh and then into Crane Pond. The water exits from Crane Pond through an outlet to the east

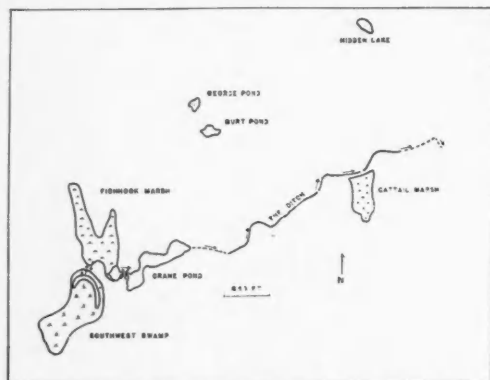


FIG. 1. Crane Pond and neighboring bodies of water studied during the course of the present investigation. Sayl Lake, not indicated on this map, is located about 400 m southwest of Southwest Swamp. Direction of water flow is indicated by arrows.

and flows eastward through a ditch until it joins a branch of Honey Creek, a tributary of the Huron River drainage system in southeastern Michigan.

Southwest Swamp, about 120 m southwest of Crane Pond, has an area of about 15 acres, of which 8 are open during periods of high water. In 1946 a semi-circular moat was dug, and this always contains water except during periods of extreme drought. Frequently the more shallow areas are dry from mid-summer until late fall.

Fishhook Marsh, about 20 m west of Crane Pond, has an overall area of 10 acres, but most of the area favorable for turtles is concentrated in an acre pond situated just west of the inlet of Crane Pond. Fishhook Marsh becomes dry during the summer.

Crane Pond (Fig. 2) is a permanent pond dug by drag-line in 1946, with an area varying from 4.5 to 5 acres. Previous to its construction, a seasonal pond was present in the same general area after 1938, when the tile draining the area was destroyed. At present the maximum depth varies from 0.7 m during extremely dry autumns to 1.3 m during the spring. The water is clear except during heavy rains. The substrate is clay, sand, and organic muck. The elevation of the pond is 274 m above mean sea level, and to the north and south are hills paralleling the southwest-northeast orientation of the pond. These hills attain an elevation of 297 m and channel the prevailing westerly winds over the pond surface.

The Ditch, 170 m east of Crane Pond, was dug in 1950 and consists of three linearly arranged ponds varying in depth from 0.3 to 1.3 m with occasional deeper holes. These three ponds contain water throughout the year although the flow of water into and out of the Ditch is seasonal. Cattail Marsh is not directly connected to the Ditch, but it is within 15 m of it. The area of the marsh is about 6 acres although the amount of open water is variable. All except a small portion of the marsh becomes dry during the summer.

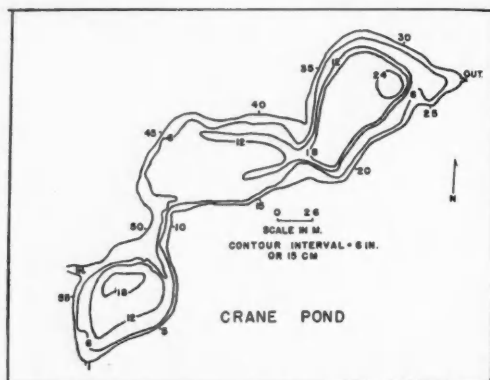


FIG. 2. Map of Crane Pond, Edwin S. George Reserve, Livingston Co., Michigan. The numbers around the periphery represent certain of the fifty-seven stakes around the pond margin. The inlet (IN) and the outlet (OUT) are shown.

Since water ceases to flow out of the Ditch into Honey Creek during early summer and resumes flowing in early winter or later, the five areas in which collecting was done are frequently isolated from the other parts of the same drainage system. This isolation must have been even more complete before 1950 when the Ditch was dug. For these reasons the area under study may be considered as a partially separate unit.

Individuals of *Chrysemys picta* inhabiting four other areas were collected during the summer of 1957. One area, Sayl Lake, is a shallow marl lake with an area of approximately 40 acres. This lake is 300 m southwest of Southwest Swamp, but there is no direct connection between the two. However, prior to 1872, Southwest Swamp drained southward, either into or close to Sayl Lake. Hidden Lake is a senescent bog lake with an area of about 2 acres. Although it is in the same drainage system as Crane Pond and related areas, Hidden Lake is separated from them by a tamarack and red maple swamp, and there is no direct passage through this swamp. Hidden Lake contains water throughout the year. Neither Island Pond nor Burt Pond, both artificial bodies, are directly connected with Crane Pond or related areas. Burt Pond has an area of about 1 acre, and Island Pond, an area of about 0.5 acre.

The most abundant aquatic plants found within Crane Pond, the area most intensely studied, are the following: (1) emergent plants—*Typha latifolia*, *Alisma triviale*, *Sagittaria latifolia*, *Leersia oryzoides*, and *Eleocharis acicularis*; (2) rooted plants with floating leaves—*Potamogeton amplifolius*, *P. natans* and *Nuphar advena*; (3) rooted plants with submerged leaves—*Potamogeton pectinatus*, *P. foliosus*, *P. amplifolius*, *Najas flexilis*, *Eleocharis acicularis*, and *Ranunculus longirostris*; (4) anchored plants with submerged leaves or thalli—*Chara* sp. and *Ceratophyllum demersum*; (5) anchored plants with floating thalli—various filamentous algae.

Other aquatic or semi-aquatic plants of lesser importance are: *Cyperus strigosus*, *Eleocharis* sp., *Scirpus cyperinus*, *Carex* sp., *Salix* sp., *Polygonum amphibium*, *P. hydropiperoides*, *Ranunculus sceleratus*, *Scutellaria epilobiifolia*, *Mentha arvensis*, and *Bidens* sp. Epizoidic algae are *Basycladia chelonum* and *B. crassa*.

The more important vertebrates associated with Crane Pond include:

Mammalia: raccoon, *Procyon lotor*; muskrat, *Onychomys leucogaster*.

Aves: pied-billed grebe, *Podilymbus podiceps*; great blue heron, *Ardea herodias*; green heron, *Butorides virescens*; American bittern, *Botaurus lentiginosus*; spotted sandpiper, *Actitis macularia*; black tern, *Chlidonias nigra*; belted kingfisher, *Megasceryle alcyon*.

Reptilia: Blanding's turtle, *Emys blandingi*; painted turtle, *Chrysemys picta*; common water snake, *Natrix sipedon*; ribbon snake, *Thamnophis sauritus*; common garter snake, *T. sirtalis*.

Amphibia: cricket frog, *Acris gryllus*; bullfrog, *Rana catesbeiana*; leopard frog, *R. pipiens*.

Osteichthyes: redbelly dace, *Chrosomus eos*; golden shiner, *Notemigonus crysoleucas*; mud minnow, *Umbra limi*.

METHODS OF STUDY

An attempt was made to collect every turtle in the population by employing the following methods: baited hoopnet traps, sunning traps, funnel traps in the inlet and outlet of Crane Pond, a retaining fence on land, noodling or muddling from a boat and on foot, use of a hand net from shore and from a boat, and seining.

The use of a dip net from a boat and from shore was very effective. An attempt was made to net throughout the entire pond within three or four collecting days, and the turtles did not appear to be greatly disturbed by collecting.

At times of low water, muddling, or feeling about in the water with the hands, was very effective from a boat. It was less desirable when depth necessitated wading, since this disturbed the rooted aquatic vegetation.

Three sunning traps were used in 1953. Each consisted of four 2 × 4 inch boards nailed together in the form of a square, 90 cm on a side. Beneath this frame was suspended a basket of 1 in mesh chicken wire into which the turtles fell when they dived off the boards. The traps were placed only in areas used as natural sunning sites or in other regions of concentration. Turtles could easily escape if the collector was not at hand, thus activity was not interrupted by a long captivity.

A retaining fence 10 in high and made of chicken wire with a mesh of 1 in was erected on land to the west of Crane Pond, and it extended for about 100 m south of the inlet parallel to the west shore of the pond. Its purpose was to detain turtles temporarily as they moved overland at that point. Escape from

this fence could also be easily accomplished if the collector was not at hand.

A very efficient trap, which took advantage of the seasonal movements of turtles, was constructed in the inlet of Crane Pond of 1 in chicken wire. A circular area of the inlet channel was surrounded by a fence of this material through which a funnel was inserted on the downstream side. The fence was 60 cm high and was supported by wooden stakes driven into the substrate. From each side of the funnel a lead fence extended downstream at an oblique angle until it passed onto shore. One lead fence joined the retaining fence described above, and the other extended onto shore for about 5 m. Thus, any turtle moving up the inlet was directed into the trap and retained there until the collector appeared. Since the current sometimes washed an opening beneath the fence, some escapes undoubtedly occurred. After the use of a simpler model in the spring of 1953, this trap was in operation continuously from early spring in 1954 until June 1955. Similar traps were used in the outlet.

A separate identification mark was given to each individual turtle when it was first captured. Each marginal lamina was assigned a number, and any combination of numbers could be given for identification merely by cutting a V-shaped notch into the free edge of the appropriate lamina with a penknife.

The data recorded at the time of capture included the identification number of the turtle, sex, date, time of day, location of capture in relation to numbered stakes placed around the periphery of the pond (Fig. 2), association with, and relation to, other animals and plants.

All turtles were released as soon as possible. This generally varied from 5 minutes to 1 hour. During periods of heavy migration, it became necessary to retain captives 12-18 hours. Turtles were always released in the immediate vicinity of capture.

Most temperatures were recorded with standard chemical thermometers and Taylor maximum-minimum thermometers. Water temperatures were taken at a depth of 30 cm, but the thermometer in the inlet was in shallower water. Wind direction was noted and the velocity measured with a Biram anemometer. This reading was taken just above the surface of the water at a location which offered the least resistance to the wind.

Since the distribution of *Chrysemys* throughout Crane Pond was associated very strikingly with that of various plants, the locations of the beds of aquatic plants were mapped. Each time a turtle was captured in Crane Pond, the type of vegetation in the immediate vicinity was recorded, and in 1954 and 1957 maps of the aquatic flowering plants and the non-planktonic algae were made at intervals throughout the year. These two methods enabled one to follow the changes in location of the plant beds for two years.

A BRIEF DEMOGRAPHIC DESCRIPTION
OF THE POPULATION

During the period of study, from March 15, 1953, until September 15, 1957, 878 individual *Chrysemys picta* were collected, marked and released. Most of the active collecting was done in or around Crane Pond, but some collecting was also done in Southwest Swamp, Fishhook Marsh, the Ditch, and Cattail Marsh. The Crane Pond section of the population was observed almost continually from March 15, 1953 to April 30, 1955. Less intensive studies were carried out from May 1, 1955 to August 20, 1955; March 23, 1956 to April 1, 1956; April 13, 1957 to April 21, 1957. Another intensive study was made from June 11, 1957 to September 12, 1957. In addition to the 878 living animals captured at least once during this period the following numbers of dead, unmarked, turtles were collected in the area: 1953, 103; 1954, 14; 1955, 1; 1956, 21; 1957, 2; total 141. A few *Chrysemys picta* were also collected at the following locations during the summer of 1957: Hidden Lake, 17; Burt and Island Ponds, 18; Sayl Lake, 34.

The proportion of marked and unmarked animals captured throughout the course of the study varied regularly after a certain point was reached (Table 1).

TABLE 1. The percentage of marked animals captured during the various times of the year. The decrease in the percentage of marked animals from the spring and fall to the summer is the result of the young animals entering the population and of the differential response of the marked and unmarked animals to the collector during the summer.

Period	Activities of the animals	Total number of animals	Percentage of marked animals
Mar. 25-May 1, 1954...	Emigrating	372	53.6
Oct. 3-Nov. 19, 1954...	Emigrating	225	84.0
Mar. 25-May 1, 1955...	Emigrating	103	76.7
June 1-Aug. 20, 1955...	Various	44	45.5
Mar. 31-Apr. 26, 1956...	Non-emigrating turtles plus dead ones	69	65.2
Apr. 15-Apr. 21, 1957...	Emigrating turtles plus dead ones	68	69.1
June 11-Sept. 15, 1957...	Various	121	54.4

During 1954 the number of turtles captured during the spring emigration was still relatively low, but during any emigration thereafter, the percentage of marked animals captured varied from 69.1 to 84.0. After the spring emigration of turtles from Crane Pond, few returned to the area until the outlying bodies of water began to dry up. The percentage of marked animals among those captured in Crane Pond during the summer varied from 45.5 to 54.4. This drop in the percentage of marked animals from the spring to the summer was almost certainly due to the different collecting techniques used. During the spring

the inlet and outlet traps were responsible for the capture of most of the animals. These traps were evidently not associated with capture by the turtles and the marked and unmarked animals did not respond differentially to them. However, during the summer when most of the animals were collected by netting from a boat, the majority of the turtles which remained at the surface as the collector approached to within three or four feet proved to be unmarked animals, while those which dove beneath the surface and swam away while the netter was still 10-15 ft away were chiefly marked individuals. This difference in the behavior of the marked and unmarked turtles increased as the study progressed. The lower proportion of marked animals during the summer was also due to the fact that the young of the year (deposited as eggs during the previous year) emerge from the nest in the spring and are first available for capture during the summer. The greatest proportion of marked turtles collected (32 of 34) was from May 19 to May 29, 1955; most of these animals were large females moving about on land during the nesting season.

On the basis of the above statements it would appear that a minimum of 69-84% of the animals in the population had been marked, and a value of 75.0% may be taken as average. There were at least 756 *Chrysemys picta* alive in 1953; 50 additional individuals of uncertain age were probably also members of this year's population. Using these figures, it can be assumed that there were roughly 1000 painted turtles inhabiting Southwest Swamp, Fishhook Marsh, Crane Pond, the Ditch, and Cattail Marsh.

These 1000 turtles were distributed over an area which varied from about 6 acres during periods of extreme drought to about 25 acres during periods of high water, although in neither case was the total area uniformly suitable for the turtles. Thus, the economic density varied from 166 turtles per acre to 40 turtles per acre. The highest density observed was an aggregation of at least 42 animals in a bed of *Potamogeton foliosus* measuring 15 × 5 m (807 sq ft)—a density of 2265 turtles per acre.

The age and sex distribution of the 756 turtles known to be alive in 1953 is shown in Fig. 3. The method by which the age of the turtles was estimated will be described in detail elsewhere (Sexton, manuscript). Briefly, it attempts to estimate the age of individual animals by comparing the medial length of the growth annuli visible on the right abdominal lamina to expected values calculated from the entire population.

Females evidently outnumber males in this population; the actual sex ratio is 1.49 ♀♀/1.0 ♂♂ for the 604 animals whose sex was known. Since some of the juveniles were not captured after they had become sexually mature, their sex could not be determined, and they were classed as juveniles. Males mature earlier than females; the sex ratio of the animals large enough to be sexually mature is 0.76 ♀♀/1.0 ♂♂.

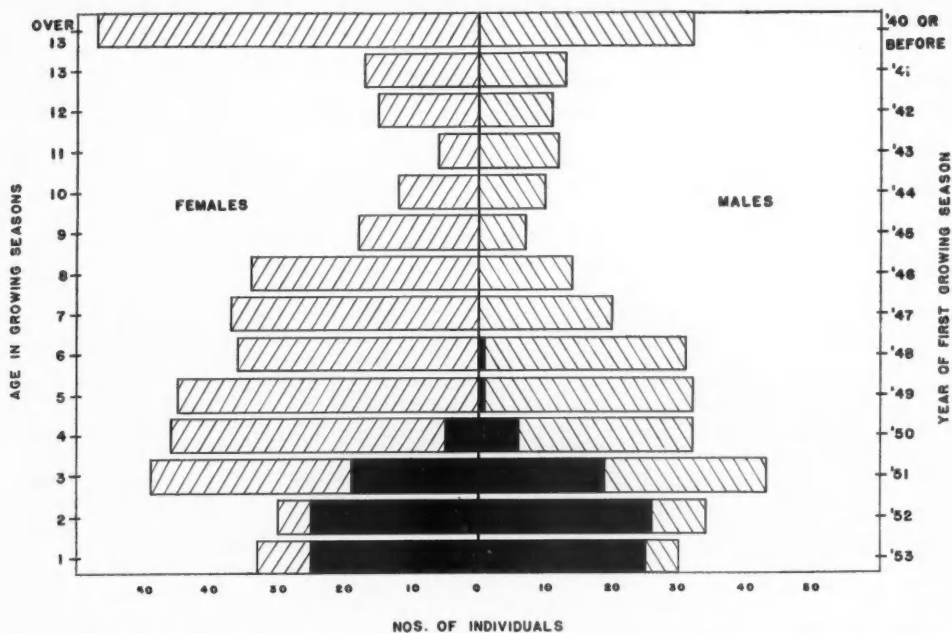


FIG. 3. The age and sex distribution of 756 individual *Chrysemys picta* inhabiting the Crane Pond area during the growing season of 1953. The solid horizontal bars represent young turtles whose sex was never definitely determined.

About 210 of the 756 animals were old enough to antedate the construction of Crane Pond in 1946. These older turtles may well have been resident in the temporary ponds and swamps which existed between 1938 and 1946. At present there is a similar situation in another part of the George Reserve. Two small, temporary ponds support about 50 turtles in their two acres during some years. These ponds become dry during mid-summer and remain so until late fall or early winter.

The remaining 546 turtles began their season of growth during 1946 or later. There has been a notable decline in the numbers of young in the two most recent age classes, but, otherwise, there seems to have been a steady population increase since the formation of the permanent bodies of water. The cause of the decline in the first and second classes has not been identified.

During the entire period of study the following minimal numbers of young-of-the-year turtles were added to the population: 1953, 63; 1954, 54; 1955, 21; 1956, 17; 1957, 12; total 167. Corresponding mortality figures are: 1953, 110; 1954, 37; 1955, 7; 1956, 61; 1957, 7; total 222. These data seemingly indicate that the population is in a slight decline, but while most remains of dead turtles (except those of very young ones) do not disappear for many months and can be found relatively easily, not enough time was spent in collecting the young-of-the-year from 1955-57 to make sure that most of these small animals were obtained. It is probably more reason-

able to compare the average natality figure for 1953 and 1954, 58 young per season, with the overall mortality rate for 1953-1957, 44 per year. Although there are still many sources of error in these estimates, the rough data would seem to indicate that the number of turtles in the population is relatively stable.

THE ANNUAL CYCLE OF *CHRYSEMYS* ACTIVITY

A BRIEF SYNOPSIS OF THE ANNUAL CYCLE

A short review of the annual cycle of the painted turtles inhabiting the Crane Pond area is presented here so that the subsequent detailed study of the spatial and temporal changes in the location of the population may be seen as parts of the entire annual cycle.

At least a few *Chrysemys* are active as soon as the ice cover begins to thaw, usually between mid-February and mid-March. During this initial cool period the movements of the animals are limited to passing back and forth from the deeper areas of the pond to the more shallow areas or to the shore. Mortality is very high at this time of the year.

As the water temperature rises, the number of active animals increases, and when the water attains 8°C, usually in late March or early April, the animals emigrate, leaving Crane Pond. Most travel westward to Southwest Swamp, but others move eastward to the Ditch. A few remain in Crane Pond. Although

most of the exodus is over within a 4-wk period, a few stragglers do not leave Crane Pond until mid-June.

A variety of activities associated with reproduction takes place during the spring. Breeding, although it may take place at other seasons, reaches a high point during the spring. It is first evident about the time that emigration begins. The turtle hatchlings, from eggs deposited the previous year, emerge from the nest cavity in mid-spring or later (Sexton 1957), but they do not emigrate. The dates on which the first hatchlings were observed for any particular year are: May 6, 1953; April 20, 1954; April 19, 1955. Nesting occurs during late May or early June, and, judging from my records, most of the females deposit their eggs within a relatively short period. Positive nesting records are as follows: June 7-June 11, 1953; May 21-May 24, 1955; June 8-June 11, 1957. These periods were usually associated with rain. Other workers have indicated that the nesting period of *Chrysemys* may be much longer. Legler (1954), on the basis of his own observations, states that nesting took place from June 16 to July 14, 1953 at Sand Lake, Nicollet Co., Minn.

During late spring and early summer most of the turtles are distributed between the bodies of water peripheral to Crane Pond: Southwest Swamp, Fishhook Marsh, the Ditch, and Cattail Marsh. As these areas begin to dry up, the animals gradually move back into Crane Pond, and by fall most of them are re-located there. This immigration is not as distinct as the spring emigration.

Growth of the animals and shedding of the laminae also occur during the summer. Recognizably new increments on the abdominal laminae are first visible between mid-May and early June. Growth ceases by the end of August.

The activities of the painted turtles may follow one of two patterns during the fall. If the water level remains low so that Crane Pond is the principal refugium in the entire area, the animals will remain here. As cold weather approaches they will move into the deeper sections of the pond. At least some of them will be active until the permanent ice cover forms in late November or early December. If, on the other hand, there is sufficient precipitation to raise the water levels of the adjacent ponds and marshes, a fall emigration will occur, and the emigrants will hibernate in the outlying areas. Those turtles which remain in Crane Pond under such conditions will emigrate the succeeding spring.

As indicated previously, the population of painted turtles living in the Crane Pond area is relatively stable in numbers, but it inhabits an environment which undergoes marked seasonal fluctuations, especially in temperature, water depth, surface area of the water, and in the nature of the aquatic vegetation. The activities of the turtles were strongly affected by these changes, and it was the purpose of this investigation to study the effects of the environmental fluctuations upon the distribution of the turtles. The behavioral pattern of *Chrysemys* and the

phenology of Crane Pond are sufficiently distinct so that five seasons may be recognized: the prevernal, the vernal, the aestival, the autumnal, and the hialmal. In this paper the seasonal activities of the painted turtles have been described on the basis of the first four of these seasons.

THE PREVERNAL SEASON

The prevernal season of the *Chrysemys* annual cycle begins with the final melting of the winter ice cover. In 1953 the ice cover began to melt during the first week of March and had disappeared by March 11 when this investigation began. In 1954 the ice cover started to disintegrate on February 16 during an unusual warm spell, and a third of the Crane Pond surface was open water by February 25. However, the waters again became completely covered with ice subsequent to February 25. The final melting of the ice started on March 13 and was completed by March 20. In 1955 melting began on March 11 and was finished by March 13. In 1956 the ice began melting at a very late date, March 31. In 1957 the exact date when melting was initiated was unobserved, but it was between March 2 and March 18. The fifteenth of March represents an approximate average for the date when ice cover is completely melted.

The end of the prevernal season is heralded by a mass emigration of *Chrysemys* out of Crane Pond. In the spring of 1953 the first emigrations were noticed on March 21. Emigration was well under way by March 25, 1954 and March 31, 1955. However, the data for 1955 are scanty, for most of the turtles had left the pond during the previous fall. The date for 1956 is uncertain, but emigration evidently occurred about April 7. Some *Chrysemys* were moving out of Crane Pond about March 18, 1957, but an unseasonal cold spell interrupted this movement, and emigration was not resumed until about April 18. March 25 is an average date for the termination of the prevernal season.

Environmental conditions during the prevernal season are such that the activities of the painted turtles are severely curtailed. A maximum-minimum thermometer located at the western end of Crane Pond registered air temperatures which ranged from -9.4°C to 15°C in both 1954 and 1955. Water temperatures during the same years varied from 1°C to 10°C . The observed maximum velocity attained by the wind roaring over the unobstructed pond surface was 380 ft/min. It is these two factors, temperature and wind, which influence the activities of the turtles very strongly during this time of the year, but other factors, such as reduced oxygen tension in the water, are also important.

During the late hialmal (winter) or prevernal periods most turtles are observed only in those places which are protected from the wind. Such protected places include ice-covered water, the lee side of shore projections, and areas protected by vegetation, such as clumps of *Typha*. The few *Chrysemys* observed in situations where they were exposed to the force of the winds during these cool periods were almost help-

less. On several occasions *Chrysemys* were found entangled in floating vegetation which had been cast up on shore or rolled up onto the shallows. Such animals were unable to escape from the debris. Turtles observed in open water were carried in the direction of the prevailing winds and could not swim against this force. One animal, seen March 16, 1955 was in shallow water and was being transported in an elliptical path perpendicular to the shore by the waves. The cloacal temperature of this animal was 7.8°C, and the velocity of the wind was 380 ft/min. Turtles collected in protected areas frequently had lower cloacal temperatures, sometimes as low as 1.4°C, but they were able to move slowly away from the investigator, indicating that they were still in control of their movement.

The *Chrysemys* observed swimming beneath the ice appeared to be trying to reach the air. One of the nine turtles observed swimming beneath the ice sheet on February 23, 1954 was moving shoreward. The water temperature was 1.5°C, and the dissolved oxygen was 6.6 ppm. The *Chrysemys* alternately extended and withdrew its head; the rostrum was pressed against the lower surface of the ice. Occasionally the mouth was opened, possibly in pharyngeal respiration. Other turtles were at the edge of the ice sheet, the head extending into the air while the body was still beneath the ice. One individual protruded his head through a small crack in the ice. Similar activities were observed during the late winter and early spring of three different years, indicating that this type of behavior is not uncommon for *Chrysemys*.

During the prevernal season the turtles move into locations where their body temperatures can be increased, that is, into shallow water or up on shore. In such situations the darkened carapace absorbs the longer wave lengths and the body temperature of the turtle may be higher than that of the surrounding medium. For example, on March 19, 1955 a *Chrysemys* captured beneath the ice had a cloacal temperature of 6.0°C while the water temperature, measured by the same thermometer, was only 4°C. This indicates that even turtles beneath the ice are absorbing enough of the longer wave lengths to raise their temperature above that of the water. Additional cases of differences between the temperature of individual turtles and that of the surrounding medium are presented in Table 2. There are four instances in which the temperature of the animal is more than 1°C lower than that of the surrounding medium, but in three of these the turtles were coming from lower, cooler depths into shallow water or up on land. There are seven turtles with cloacal temperatures within 1°C of the medium; the cloacal temperature of the remaining 14 *Chrysemys* is more than 1°C above that of the surrounding medium, in some cases 10° or more higher. The greatest discrepancies in temperature occur in those animals which are sunning on the shore.

The movements of the painted turtles within Crane Pond appear to be relatively limited during this

TABLE 2. Cloacal temperatures of *Chrysemys* active during the prevernal and early vernal season compared with the temperature of the medium in which each individual was captured. The temperature of the medium was measured twice, once with a black cloth wrapped around the thermometer bulb to simulate the dark carapace and once without it.

Date	Activity	TEMPERATURE IN °C		
		Cloaca	Medium	
			Bulb not blackened	Bulb blackened
March, 1955				
11.....	Sunning on shore	10.4	12.8
11.....	Just on shore	8.6	9.8
13.....	Sunning on shore	19.8	9.8
	Resting in water	9.2	8.0
	Swimming	8.0	9.4
	Sunning on shore	15.0	15.4
	Just crawled up shore	10.2	14.6
14.....	Sunning on shore	27.0	10.2
16.....	Sunning on shore	10.0	10.6	17.4
	In water	7.8	7.0
19.....	In water under ice	6.0	4.0	5.6
	Sunning on shore	14.6	8.8	20.8
20.....	Sunning on shore	32.0	20.0	29.1
	In water	8.0	6.8
21.....	Sunning on shore	8.0	7.4	12.2
28.....	Sunning on snow	8.4	4.3	16.4
29.....	Sunning on shore	24.0	15.9	24.2
30.....	Sunning on shore	27.9	16.4	25.2
March, 1956				
31.....	In water under ice	5.0	2.8
	In water under ice	1.6	1.6
	In water under ice	1.4	1.2
	In water under ice	1.4	1.0
April, 1956				
1.....	In water under ice	2.9	1.4
	In water under ice	4.6	2.4
April, 1957				
15.....	Sunning on shore	13.8	11.8

period of late winter and early spring. In 1954 five *Chrysemys* were captured two or more times before the advent of emigration; the minimal direct distance between farthest points of capture within any one activity area varied from 3.4 to 124 m, averaging 41 m. During the analogous in 1955 seven *Chrysemys* were captured two or more times. The distances between farthest points within a single activity area varied from 9.2 to 92.3 m and averaged 45 m.

THE VERNAL SEASON

The vernal season extends from March 26 to May 31. The criterion by which the first date was selected has been mentioned previously. The vernal season is concluded when certain submerged aquatic plants which are important to *Chrysemys picta* grow to the

water surface. In 1953 *Chara* sp. was first observed at the surface of Crane Pond on June 1; *Ranunculus longirostris* and some other species had attained the surface by June 14, but they had probably been at the surface somewhat earlier than this. In 1954 *Chara* sp., *Potamogeton foliosus*, *P. pectinatus*, and *Ranunculus longirostris* became evident at the water surface between May 20-26. In 1955 *Chara* sp., *Potamogeton foliosus*, and *Ranunculus longirostris* grew to the surface between May 13-19. In 1957 *Potamogeton foliosus*, *P. pectinatus*, *Ranunculus longirostris* and various species of filamentous algae were at the surface by June 15. These various dates indicate that May 31 is about the time aquatic plants in Crane Pond reach the surface of the water and form extensive floating mats of leaves and thalli.

This period is characterized primarily by a mass emigration of most of the *Chrysemys* in Crane Pond to surrounding bodies of water and by the localization of those turtles remaining in Crane Pond to certain areas in which there are sunning sites. These two occurrences, the emigration and the localization, are evidently related to the lack of surface vegetation in Crane Pond at this time of year. Other events which characterize this season are the initiation of feeding, mating activities, and the emergence of the hatchling turtles from the nests of the previous year. Nesting takes place during the end of the vernal season and the beginning of the aestival one.

The temperature is very variable during the vernal season, even if it is increased over that of the prevernal season, and the wind velocity can be quite high. During 1954 the air temperature at the western end of Crane Pond varied from -12°C to 32.5°C . Air temperatures below 0°C were commonly recorded throughout the vernal season of 1954, the last such low temperature being recorded between May 25-28. No maximum-minimum thermometers were kept in the water during 1954. The winds attained velocities of at least 740 ft/min just over the water surface. The vernal season of 1955 was much more placid than that of the preceding year. The air temperatures

varied from -3° to 30°C . There were few times when the air temperature fell below 0°C in 1955, the last time being between May 10-14. The water temperatures during the same year ranged from 6°C to 26°C in the vernal season. The maximum wind velocity was 480 ft/min.

Throughout this study the term migration will be used to signify "... a movement which involves a journey into a definite area, and a return journey to the area whence the movement arose ..." (Heape 1932). An emigration will be a movement away from Crane Pond, and an immigration will be a movement into Crane Pond.

The vernal emigration and the emigrants. The annual activity cycle of the *Chrysemys* population in the Crane Pond area includes at least one migratory movement although all animals do not appear to participate in the migration. Typically, the emigration takes place during the vernal season, the emigrating turtles heading eastward and westward away from Crane Pond (Table 3). The hills rising 20-25 m and more above the pond surface to the north and south preclude any extensive movements in these directions. The animals disperse either by traveling overland or by moving through the inlet or outlet. Those going overland eastward from Crane Pond probably are soon funneled into the outlet by the topography. Indeed, all turtles moving eastward through the outlet must first cross a narrow piece of land, about 12 m wide, before entering the outlet proper, for they will not pass through the buried culvert which drains the pond. Turtles migrating overland towards the west must travel across a minimum of 120 m of grassland before attaining Southwest Swamp. Those which emigrate through the inlet remain in water for most of the journey to Southwest Swamp, but they first cross a road which is 5 m wide separating Crane Pond from Fishhook Marsh and then cross a minimum of 40 m of land to reach Southwest Swamp. It is possible to travel between the swamp and the marsh without crossing such an extensive tract of land, but there is no definite water

TABLE 3. Numbers of turtles moving into and out of Crane Pond during the various seasons. The seasons are abbreviated as follows: P, prevernal; V, vernal; Ae, aestival; Au, autumnal. The dashes indicate periods when the traps were not in continual operation.

	YEAR AND SEASON											
	1953				1954				1955		1957	
	P	V	Ae	Au	P	V	Ae	Au	P	V	V (part only)	
Turtles Leaving Crane Pond by Moving:												
West through the Inlet.....	16	37	0	0	2	277	12	175	12	61	35	
West Overland.....	2	3	0	0	1	20	1	5	0	0	20	
East through the Outlet.....	—	—	0	—	—	9	6	6	0	15	—	
East Overland.....	0	0	0	0	0	4	1	0	0	0	—	
Turtles Entering Crane Pond by Moving:												
East Overland.....	0	0	0	3	0	1	6	5	0	2	—	
West through the Outlet.....	—	—	0	—	—	6	15	7	0	2	—	

channel between the two areas. The turtles do not seem to favor this route, for none has ever been captured using it. Hence, all migrants cross some land.

The number of *Chrysemys* movements through the inlet during emigration is shown in Table 4. These data do not represent the total number of individual turtles passing through the inlet, for some emigrated through once, only to return to Crane Pond and then travel up to the inlet again. In the vernal season of 1954, 13 *Chrysemys* moved out of Crane Pond twice, 2 three times and 1 four times. The movement made during the fall of 1954 will be considered later.

TABLE 4. The numbers of *Chrysemys* emigrating westward through the inlet during the spring of 1954 and 1955. Only those dates are indicated on which turtles were captured in the inlet.

March	1954	1955	April	1954	1955
12	0	2	15	7	0
14	0	2	17	12	1
15	0	5	18	0	1
18	2	0	19	0	3
20	0	1	21	15	1
21	0	2	22	0	1
25	10	0	24	1	0
27	1	0	25	1	0
28	24	0	26	2	0
29	0	1	29	2	0
30	0	2	30	0	1
31	0	11			
April			May		
1	1	5	1	4	0
2	3	10	12	1	0
3	0	2	14	1	0
4	0	0	15	1	0
5	7	7	21	1	0
6	43	0	June		
7	69	0	1	1	0
9	3	6	5	2	0
10	1	2	6	1	0
11	22	0	10	2	0
12	6	3	21	3	0
13	17	4	22	1	0
14	23	0	July		
			5	1	0

The numbers of movements in the migration rapidly reach a peak and then diminish, but the emigration may continue in a desultory fashion well into the aestival period. These stragglers may be moving about at random within the lower areas of the Reserve so that it could be erroneous to consider them here, but they are included for completeness.

The percentage of juveniles, adult males, subadult females, and adult females emigrating through the inlet is presented in Table 5. Juveniles are those animals which have an abdominal laminar length less than 2.0 cm and whose sex cannot be readily determined. They are sexually immature. Adult males are those *Chrysemys* with an abdominal laminar length of 2.0 cm or more and which have elongated claws on the forelimbs (Sexton, manuscript). Subadult females are those painted turtles having an

abdominal lamina whose length is between 2.0 and 2.9 cm and which do not have elongated claws. They are sexually immature. Adult females are those turtles in which the length of the abdominal lamina is greater than 2.9 cm and which do not have elongated claws. The majority of these are sexually mature. As a basis for comparison the 756 individual *Chrysemys* known to be alive during the 1953 growing season (Fig. 3) consisted of 32.8% juveniles, 20.3% subadult females, 20.2% adult females, and 26.7% adult males. Constant check was not maintained over the emigration during 1953 and 1957 so that the data for these two years are incomplete. In the spring of 1954, 19.3% of the emigrants were juveniles, 21.4% subadult females, 29.6% adult females and 29.6% adult males. In 1955 11% of the emigrants were juveniles, 21.9% subadult females, 34.2% adult females and 32.9% adult males. It can be seen that fewer juveniles emigrate than one would expect on the basis of chance, but more adult females and males emigrate. The percentage of subadult females in the entire 1953 population and in the population of emigrants is about the same.

The data from Table 5 indicate that a large portion of the smaller turtles remains in Crane Pond while the larger individuals of both sexes emigrate. Several collections were made in the pond during periods of heavy emigration to determine the structure of the residual population. During April 9, 1953 there was an emigration of 27 *Chrysemys* of which 3.7% were juveniles, 14.8% subadult females, 25.9% adult females, and 55.6% adult males. On the same day 11 painted turtles were netted within the pond, and these consisted of 72.7% juveniles, 9.1% subadult females, and 18.2% adult females. During April 6 and 7, 1954, 112 turtles were caught in the inlet and 14 in the pond. The emigratory group consisted of 14.3% juveniles, 19.6% subadult females, 34.8% adult females, and 31.3% adult males. The residents were composed of 71.4% juveniles, 7.1% subadult females, and 21.5% adult females. Even though the numbers of turtles captured within the pond is small, the results seem to corroborate the belief that the younger turtles do not tend to emigrate.

There is also a tendency for more females to emigrate than males. Whereas the sex ratio of the adult animals in the 1953 population of 756 *Chrysemys* was 0.76 ♀/1.0 ♂, that of adults emigrating through the inlet during the spring of 1954 was 1.0 ♀/1.0 ♂ and that for the spring of 1955 is also 1.0 ♀/1.0 ♂. Hence, it would appear that although proportionately more adult *Chrysemys* are among the emigrating group than one would expect, the two sexes respond differently. The change in the sex ratio is evidently brought about by the increased number of adult females which emigrate.

The relative abundance of each of these four classes, juveniles, subadult females, adult females, and males, did not remain constant throughout the emigratory period (Table 6). In 1954 the adult

TABLE 5. Composition of the total number of painted turtles emigrating through the inlet.

	Mar. 21-May 27 1953		Mar. 18-May 31 1954		Oct. 3-Nov. 19 1954		Mar. 12-Apr. 30 1955		Apr. 17-21 1957	
	No.	%	No.	%	No.	%	No.	%	No.	%
Juveniles.....	3	5.7	54	19.3	35	19.9	8	11.0	1	3.0
Males.....	24	45.3	83	29.6	53	30.1	24	32.9	15	45.4
Subadult Females.....	8	15.1	60	21.4	43	24.4	16	21.9	4	12.1
Adult Females.....	18	33.9	83	29.6	45	25.6	25	34.2	13	39.4
Total.....	53	100.0	280	99.9	176	100.0	73	100.0	33	99.9

TABLE 6. Composition of the emigrants moving westward through the inlet.

Date in 1954	COMPOSITION OF MIGRANTS IN %				Total No.
	Juv.	♂♂	Subad. ♀♀	♀♀	
Mar. 25.....	10.0	20.0	20.0	50.0	10
Mar. 28.....	4.2	41.7	8.3	45.8	24
Apr. 6.....	7.0	44.2	11.6	37.2	43
Apr. 7.....	18.8	23.3	24.6	33.3	69
Apr. 11.....	9.1	18.2	45.4	27.3	22
Apr. 13.....	35.3	11.8	29.4	23.5	17
Apr. 14.....	26.1	21.7	30.4	21.8	23
Apr. 17.....	41.7	33.3	16.7	8.3	12
Apr. 21.....	66.7	13.3	13.3	6.7	15
Oct. 12.....	25.4	27.0	14.3	33.3	63
Oct. 13.....	25.8	29.0	29.0	16.2	31
Oct. 14.....	6.3	50.0	25.0	18.7	16
Oct. 23.....	0.0	9.0	54.6	36.4	11
Nov. 19.....	27.3	18.1	27.3	27.3	11

females were the first to reach their peak of abundance, relatively early in the emigration. The males attained their greatest relative abundance shortly afterwards, and the males were followed by the subadult females which reached a maximum on April 11. The percentage of juveniles among the emigrants was erratic during the early part of the emigration but increased greatly towards its end. It is interesting to note that the sequence of these four classes in emigration is the same as the descending order of abundance of these four classes in the overall make-up of the emigrants. That is, the adult females are the first to emigrate in numbers, and relatively more females emigrate than do members of any other class.

The relative abundance of these same four classes among the emigrants leaving Crane Pond by other routes is presented in Table 7. Unfortunately, these data are tenuous since the absolute numbers passing out of Crane Pond through these other egresses are low. Even so, it appears that the juveniles do not leave the pond by moving through the outlet or by going overland, and it appears that relatively high proportions of adult males and females (compared to the animals alive in 1953, Fig. 3) do utilize these other paths. The relative abundance of the subadult females varies a great deal year to year and exit to exit.

Environmental features of Crane Pond and surround-

ing areas during the vernal emigration. There is little surface vegetation present in Crane Pond during

TABLE 7. The composition of emigrants leaving Crane Pond via various routes.

	West through the inlet	West overland	West through the inlet	West overland	West through the inlet	East through the out- let
	1954	1954	1957	1957	1955	1955
Total number of turtles	280	21	33	20	73	15
Percent Juveniles.....	19.3	4.9	3.0	5.0	11.0	13.3
Percent Subadult						
Females.....	21.4	33.3	12.1	15.0	21.9	26.7
Percent Adult Females	29.6	33.3	39.4	45.0	34.2	20.0
Percent Adult Males..	29.6	28.5	45.4	35.0	32.9	40.0

the vernal season, for *Nuphar advena* is the only species which grows to the surface much before the end of the spring. This species was first apparent on the water about April 14, 1954 and March 9, 1955. The majority of the plants reached the surface and filled in most of the outline of each lily bed by May 6, 1954 and April 22, 1955. This same condition, lack of surface vegetation, does not prevail in Southwest Swamp during the vernal season. Here the area contained within the confines of the moat resembles Crane Pond, but the shallow areas of the Swamp support a relatively high concentration of surface vegetation, including such plants as *Leersia oryzoides*, *Sparganium eurycarpum*, *Alisma triviale*, *Sagittaria latifolia*, *Spirodela polyrhiza* and *Lemna trisulca*. During the vernal season many of these plants, especially the graminoids, do not project above the water. Rather, the distal ends of the plants float upon the surface, forming a mat. *Spirodela polyrhiza* becomes entangled in this mat and provides additional cover.

A temperature gradient exists within Crane Pond. The thermal variations of the inlet current were compared to those recorded at other stations throughout the Pond. During the prevernal and vernal seasons a maximum-minimum thermometer was placed in the water at each of the following stations: the inlet, stakes 57, 13, 32, and 26 (Fig. 2). During this period the inlet registered the greatest difference between maximum and minimum temperatures in 15 of 24 times. In 5 of the remaining 9 cases, the dif-

ference obtained at the inlet was as great as that obtained elsewhere so that there were only four days in which the difference between the two extreme temperatures at the inlet was less than that obtained at other points in the Pond. Evidently, the shallower water in Fishhook Marsh is heated more quickly during the day and cools more rapidly during the night. As this water flows into Crane Pond a thermal gradient is established which is reversible, for the inlet current is warmer than the water in Crane Pond during parts of the day but cooler at night.

In addition, the difference between maximum and minimum values recorded at stake 57 was greater than the difference for similar recordings at stake 13 a total of 11 times out of a possible 14. This indicates that at least the western third of the Pond is divided thermally. The inlet current has the most variable temperature, and the water off stake 57 is less variable than that in the inlet but more so than that off stake 13.

Fluorescein and crystal violet added to the inlet current indicated that the water passing through the main channel of the inlet bifurcated into two branches soon after leaving the *Salix* zone which delimits the mouth of the inlet. One branch continues eastward into Crane Pond or moves parallel to the north shore. The distance over which this water mass will retain its integrity within Crane Pond is not known, for the dyes become dissipated too quickly. However, the dye is evident for a distance of 10 m from the inlet mouth. The second branch made a sharp turn southward and continued about 3 m off the western shore for 20-25 m.

The influence of water temperature and current on emigration. *Chrysemys* is primarily a diurnal animal, and emigration is restricted to the daylight hours (Table 8). The data in Table 8 indicate that the daily peak in emigration during the vernal season, measured in number of turtles emigrating per hr,

TABLE 8. The hourly variation, in number of *Chrysemys* emigrating per hour, on those days during 1954 on which 15 or more *Chrysemys* moved westward through the Crane Pond inlet. The question marks refer to data for which the rate cannot be accurately determined although some emigration occurred.

Time in hours	Mar. 28	Apr. 6	Apr. 7	Apr. 11	Apr. 13	Apr. 14	Apr. 21	Oct. 12	Oct. 13	Oct. 14
6-7					0.0	0.0			?	?
7-8			?		2.7	2.0	?		3.0	2.3
8-9		?	3.0		2.7	2.0	0.4	?	3.0	2.3
9-10		1.3	3.0	?	2.7	1.7	0.4	8.5	1.0	2.3
10-11		1.3	0.5	1.0	2.2	1.7	0.4	8.5	2.0	1.0
11-12	0.0	1.3	0.5	1.0	2.2	1.7	0.4	10.3	2.0	1.0
12-13	9.5	10.0	11.5	7.0	2.2	3.2	0.4	10.3	8.5	1.0
13-14	9.5	10.0	11.5	7.0	2.2	3.2	2.0	10.3	8.5	1.0
14-15	2.0	10.0	27.0	3.0	0.0	3.2	5.0	0.4	?	?
15-16	1.5	7.0	3.0	0.0		3.2	5.0	0.4		
16-17	1.5	0.3	3.0			0.3	0.0	0.4		
17-18	0.0	0.3	0.0			0.3		0.4		
18-19		0.3				0.3		0.4		
19-20		0.0				0.0		0.0		

occurred most frequently between 12 noon and 3:00 pm.

Little or no emigration took place unless the water temperature in the inlet rose above a certain critical level. This level was 7°C in 1954 and 6°C in 1955. However, 8°C appears to be the lowest water temperature at which *Chrysemys* migrate in numbers (Table 9). The discrepancy between cloacal temperature

TABLE 9. Relationship between the number of emigrants moving through the inlet and the temperature of water at the inlet.

	Inlet Water Temperature in °C																
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20 and over	
	Number of Turtles																
Spring 1954.....	0	0	2	31	0	17	1	11	5	36	0	1	50	0	0	0	
Fall 1954.....	2	3	2	2	2	9	0	11	8	0	2	12	28	21	0	0	
Spring 1955.....	0	2	2	4	5	2	1	12	7	2	11	6	2	1	1	3	

and the temperature of the medium which was noticed during the prevernal season (Table 2) was not as extreme in the emigrating *Chrysemys* (Table 10). No turtle captured in the inlet had a cloacal temperature below 8.4°C. These data again indicate that there is a threshold, approximately 8°C, below which emigration does not occur.

TABLE 10. Contrasts in temperature between individual emigrating *Chrysemys* and surrounding medium. Asterisks indicate animals which had been in the air.

Water Temperature of the Inlet °C	Cloacal Temperature of the Turtles °C
6	8.7, 8.8
7	8.9
8	8.4, 8.6
8	8.5, 9.0
10	11.3
11	11.7
11	11.8
12	13.4
13	14.4
13	13.2, 14.2, 14.3, 15.0, 15.2, 21.2*
14	14.6
14	16.1
15	15.7
15.5	15.8, 15.9, 15.9, 16.1
15.5	16.2, 16.7, 27.0*
15.5	16.1
15.5	16.0
18	18.7
19	21.0
20.5	21.5

Table 11 shows that certain temperatures must be attained in both the inlet water mass and the water within Crane Pond before emigration will occur. During the short period in which emigration was studied in 1957 one maximum-minimum thermometer was placed in the inlet and another just beneath the

surface of the water within Crane Pond at a point 48 m east of the inlet mouth and 15 m off stake 9. The water was 57 cm deep at this position. *Chrysemys* did not emigrate in numbers until both the minimal and maximal temperatures were above 9-10°C at both places.

TABLE 11. The number of emigrants and the minimal and maximal water temperatures in the inlet and in Crane Pond between April 15 and April 20, 1957. A maximum-minimum thermometer was placed in the inlet for this entire period, and another was situated just beneath the surface of the water at a point in Crane Pond 48 m west of the inlet mouth.

Date	WATER TEMPERATURES °C				NUMBER OF EMIGRANTS	
	Inlet		Crane Pond		West through Inlet	West Over-land
	Max.	Min.	Max.	Min.		
April 15....	14	3	11	2	0	0
April 16....	10	5	10	6	0	0
April 17....	11	8	10.5	8	0	0
April 18....	12	9	12	9	2	0
April 19....	19	10	17	10	12	13
April 20....	21	15	20	14	16	7

Figure 4 illustrates the reversal of the thermal gradient within the western part of Crane Pond. The curve for the temperature of the inlet water rises more steeply than that of the water off stake 57 or the former crosses the latter during the morning. Emigration is heaviest when the curve for the inlet temperature is above that of the pond temperature. Perhaps it is this phenomenon of thermal reversibility which accounts for the peak in the diel cycle of emigration occurring in the afternoon, for few turtles move out before the temperature polarity has been

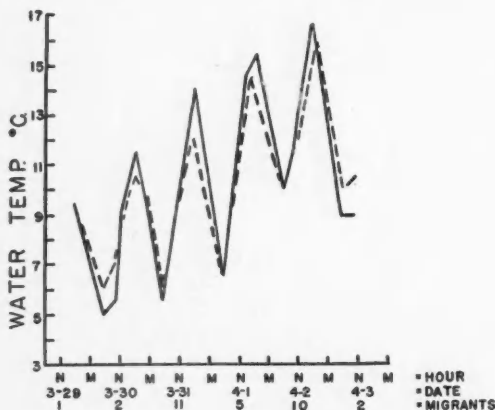


FIG. 4. Relationship of the water temperature of the inlet (solid line) and that of Crane Pond (dashed line), as represented by the water off stake 57, to the number of emigrants passing up to the inlet. N is noon and M is midnight. The data are from the spring of 1955.

reversed, and many do not exit before it is well established.

While the exodus of the *Chrysemys* is correlated with certain temperature characteristics of the various water masses, there are indications that the current itself is a positive force influencing emigration. No mass departure of turtles from the Pond was ever observed except during periods when water was flowing into the Pond from the west. Such occasions occurred during the springs of 1953, 1954, 1955, 1957 and in the fall of 1954. Actually, they undoubtedly take place each spring and in those autumns in which water enters Crane Pond. During the latter part of April, 1955, the inlet current was blocked to see if there was any change in the numbers of *Chrysemys* emigrating or if there was any diminution in the activity of the animals about the inlet mouth. Most of the time the current could not be stopped, but it was reduced to at least half speed. Several times there was no flow of water through the inlet at all. These experiments were very inconclusive since most of the animals had already left Crane Pond so that too few turtles were captured to make any generalizations. However, shortly after the removal of the dam on April 16, there was an increase in the amount of activity about the mouth of the inlet although most of the turtles seemed to be seeking basking sites. The experiment was repeated on April 21, 1957. This day had been preceded by two days on which fairly extensive emigration had occurred. The current was blocked at 8:20 am on the 21st. The dam did not interfere with the movement of the animals into the trap. No *Chrysemys* were in the inlet trap at this time; the water temperature was 15.5°C, certainly adequate for emigration. No turtles were found in the trap at 10:35 am (water temperature = 17°C) nor at 11:45 am (water temperature = 19°C). There were 4 *Chrysemys* sunning at the mouth of the inlet and 6 in the water off the inlet at this latter time. The block was removed at 12:30 pm (water temperature = 19°C) and rechecked at 1:00 pm, but there were no turtles in the trap. One *Chrysemys* was captured at 1:30 pm (water temperature = 20.5°C), an *Emys blandingi* at 2:30 pm and a second *Chrysemys* at 3:45 pm (water temperature = 22°C). The data are extremely meager, but they at least are in keeping with the idea that the current itself is a factor in directing the emigrating *Chrysemys* to move westward.

The extent of the dispersal movements. Turtles from all parts of Crane Pond emigrate through the inlet, and the minimum direct distance a turtle must travel within the pond before reaching the inlet varies from 0. m if the animal is at the inlet mouth to 315 m if it is at the eastern end of Crane Pond. In 1954, 22 *Chrysemys* were captured a total of 27 times in Crane Pond before they were again captured while emigrating through the inlet. The minimum direct map distance between the site of original capture and the inlet mouth was 41 m, the maximum 315 m, the average 156 m. The shortest time interval between the

original capture within Crane Pond and the capture in the inlet was 3 hours and 15 minutes (the minimum map distance traversed was 120 m), the longest span was 43 days (two cases: the distance traversed was 65 m in one instance and 295 m in the other), and the average interval was 16.5 days.

There is no evidence that the painted turtles closest to the inlet mouth are the first to emigrate. Three painted turtles were captured two or more times in Crane Pond prior to their emigration. All three had moved away from the inlet rather than moving directly to the inlet. In addition, when tested for any correlation between them, the two variables, minimum map distance between the site of the original capture within Crane Pond and the inlet mouth and the time interval between the original capture and the inlet capture, were shown to be independent with $r = 0.24$ and $N = 22$.

The main areas into which *Chrysemys* journeys from Crane Pond are to the west and southwest and to the east of Crane Pond. Southwest Swamp supports many individuals of this species, most of them from Crane Pond. This necessitates a journey of at least 120 m to reach Southwest Swamp and a movement of another 280 m to reach the most distant point of the Swamp. Other *Chrysemys*, previously marked in Crane Pond, have been recaptured in the Ditch, 1,080 m downstream from Crane Pond and on a hillside east of Cattail Marsh, about 1,000 m downstream from Crane Pond.

The dispersal of *Chrysemys* from Crane Pond seems to be limited to Southwest Swamp, Fishhook Marsh, the Ditch, and Cattail Marsh. During the summer of 1957 four bodies of water peripheral to the Crane Pond area, Hidden Lake, Island Pond, Burt Pond, and Sayl Lake (Fig. 1), were investigated to see if any marked animals from the Crane Pond area had moved into them. Although the first three areas are within the same drainage system as Crane Pond, there is no direct water channel which connects them to Crane Pond. During periods of high precipitation water from Hidden Lake and Burt Pond flows into the Ditch after passing through extensive marshes and swamps. None of the 17 *Chrysemys* captured in Hidden Lake, 12 juveniles, 3 subadult females, 1 adult female and 1 adult male, were animals which had been marked previously. Nor were any of the 18 painted turtles collected in Burt and Island Ponds from Crane Pond. These 18 animals consisted of 6 juveniles, 2 subadult females, 7 adult females, and 3 adult males. Sayl Lake is 400 m southwest of Southwest Swamp and separated from it by a road and by dry ground. The total distance between Crane Pond and Sayl Lake is about 800 m. None of the 34 *Chrysemys* captured in Sayl Lake were recaptures from the central population.

Activities of the Chrysemys remaining within Crane Pond. Only a few turtles remain within Crane Pond for the entire vernal season. Counts of turtles were made in the spring of 1954 to give some indication of their relative abundance in Crane Pond in contrast to their abundance in the northern one-fifth of

Southwest Swamp. On May 1, 11 *Chrysemys* were counted in the Swamp and only 1 in the Pond; May 6, 8 in the Swamp and 0 in the Pond; May 9, 3 in the Swamp and 0 in the Pond; May 13, 22 in the Swamp and 4 in the Pond.

It became evident that the distribution of *Chrysemys* remaining in the Pond was correlated with certain environmental factors. On April 22, 1955, a map of the surface vegetation of the pond was drawn, and on April 23 the location of all of the *Chrysemys* observed in the pond was superimposed on this background map (Fig. 5). The location of painted turtles captured or observed during May 1953 was also recorded on this map. In comparing the distribution of the animals during these two vernal seasons, it becomes apparent that there are four areas of turtle concentration common to the two maps. The use of these four areas by *Chrysemys* appears to be related to the fact that these areas provide the only sunning sites at this time of year. One section, indicated by the fallen trees, has shifted slightly over the two year period. In 1953 there were only a few fallen limbs which were exposed enough to provide sunning areas. During the spring of 1954 two large oak trees toppled into the water, and these formed more desirable sunning places. A second area used by the *Chrysemys* is the *Typha* bed. The clumps of dead *Typha* projecting above the water surface provided platforms suitable for sunning. The dead *Salix* in the mouth of the inlet is the third area of concentration. The fourth area, in the west section of the pond, is the beds of *Nuphar advena* whose floating leaves provide sunning stations. In 1955, the turtles were also associated with the mats of filamentous algae which grew alongside and within the patches of *Nuphar*. It is noticeable that few *Chrysemys* were found in those areas lacking sunning sites. During the vernal season the banks were not used for sunning as frequently as they were during the prevernal season.

The minimum distances between farthest points of capture were measured for *Chrysemys* captured two or more times within Crane Pond during the late vernal seasons of 1953 and 1954. The limiting dates were arbitrarily set at April 15 and May 31 so that movements due to emigration could be more or less eliminated. Nine painted turtles were captured two or more times during this 6-wks period in 1953; the distances ranged from 0 m to 301 m and averaged 144 m. Eight turtles were collected during the same period in 1954; the range of variation was about the same as in the previous year, 1 m to 279 m, but the average was only 63 m. Both of these averages are higher than those observed for the prevernal season.

Chrysemys begins to feed when the temperature of the water rises above 15°C. Animals were observed eating in Crane Pond at temperatures of 16°C and 17°C. Turtles from areas within 10 km of the George Reserve were kept in captivity in a large pool under fairly natural conditions. Feeding became extremely desultory as the falling temperature approached 15°C.

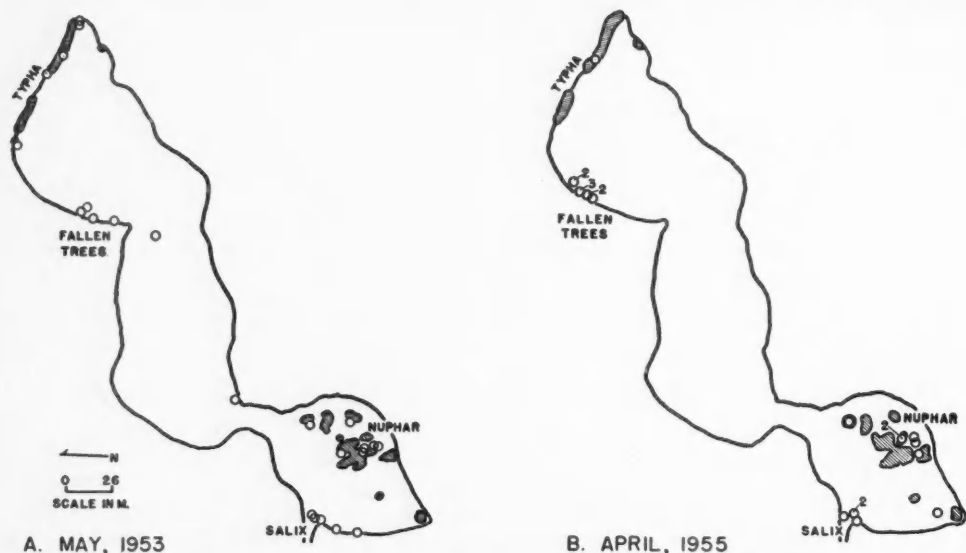


FIG. 5. Location (circles) of all individual *Chrysemys* observed in Crane Pond in May, 1953 and April, 1955. Each circle represents a single individual except as indicated by the attached numbers.

THE AESTIVAL SEASON

This period of the year extends from June 1 until August 31, although there may be a leeway of one or two weeks in either direction. As mentioned previously, most of the aquatic plants which are important to the painted turtles as loci of activity have reached the surface by June 1. The vegetation continues to increase in weight as the season progresses until the biomass of the air-dried non-planktonic vegetation averages at least 1300 kg per acre by mid-July. The air and water temperatures attain their annual maximum during this season. In 1954 the air temperature at stake 57 varied from a minimum of 2°C to a maximum of 35°C during this period. The water temperatures are less extreme. In 1954 the minimum water temperature registered 13°C, the maximum 29°C. In 1957 the temperature of the surface water (shaded) ranged from 17°C to 33°C while the temperature on the bottom of the pond in water 53-65 cm deep varied from 18°C to 31°C. Thus, the water temperature rarely falls below 15°C during the aestival season. This is the temperature at which *Chrysemys* begin to feed. Renewed growth of the animals is first noted during the first week or two of the aestival season and continues until late August. Shedding of the laminae or scutes also occurs during this time of the year.

The activities of the painted turtles during this season are characterized by dispersal movements from one body of water to another and by movements from areas of one vegetation type to another within a single pond as the water depth fluctuates and the nature of the surface vegetation changes.

Spatial reorganization of the population. There is no mass immigration of *Chrysemys* which can compare

in intensity with the emigration, for the animals gradually filter back into the pond from outlying areas. If one assumes that the first aestival recapture in Crane Pond of a known vernal emigrant indicates the latest date by which that individual returned to Crane Pond, one can obtain some evidence of the intensity and duration of the immigratory movement. The dates on which known emigrants were recaptured after returning to the pond indicate that immigration is a steady process which begins during the emigration period itself and extends into fall (Figure 6). It is also indicated that the height of the immigration probably occurred during the latter half of July and most of August in 1954. There is a three-week period in late August and early September for which there are no data.

The entire migratory cycle in *Chrysemys*, then, consists of a sharply peaked movement out of the pond during the spring (occasionally the fall) and a gradual movement back into the pond in the summer. The peak in the former is very pronounced and occurs soon after the start of the exodus. There is no distinct peak in numbers of returning animals. Table 3 shows the number of animals caught entering or leaving the pond during the course of the study. It can easily be seen that most of the animals caught in the spring are leaving the area, while a higher proportion of those captured during the summer are returning. This is true not only for the inlet but also for the outlet. Actually the six animals moving eastward out of Crane Pond in the aestival season of 1954 and ten of the twelve turtles leaving via the inlet that same season were stragglers from the vernal emigration. These sixteen turtles left during the first three weeks of June. In the vernal

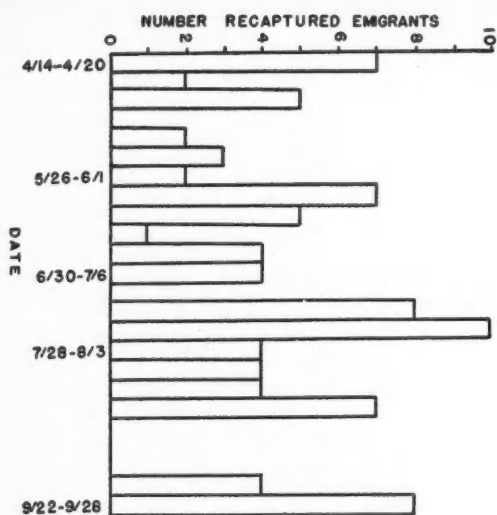


FIG. 6. The return of vernal emigrants to Crane Pond during the summer of 1954. The ordinate represents the number of emigrants recaptured in Crane Pond after they had emigrated, and the abscissa the week during which any emigrant was first recaptured in the pond. No collecting was done from August 25 until September 16.

season of 1954 the greater number of *Chrysemys* moving through the outlet are headed eastward away from the pond. In the aestival period the trend through the outlet is reversed, for most of the painted turtles are now moving westward into the pond.

Response of the population to vegetation changes. During the aestival season of 1954 three censuses were made of the *Chrysemys* in Crane Pond. There were 22 individual *Chrysemys* counted on June 1 during the first census, 71 on June 22 during the second census, and 152 on August 13 during the final census. This increase in numbers of turtles as the summer progressed also indicates that turtles return to Crane Pond during the aestival period.

The census of June 1 did not include mapping of the actual position of each individual, but 3 were sunning on exposed branches, 2 were swimming in open water, and 17 were associated with aquatic vegetation, mostly *Ranunculus longirostris*, *Potamogeton foliosus*, and *P. strictifolius*.

Prior to the second and third censuses in 1954, maps of Crane Pond were made depicting the areas of open water and of surface vegetation. In addition, each plant bed was described by species so that an accurate picture was formed of the vegetation within the pond at the time of each census. The position of each turtle was superimposed on these base maps. A similar map was made on June 15, 1957, and 78 *Chrysemys* were observed.

In examining the maps, it became apparent that the turtles were not distributed at random in relation to the pond surface but were clumped in those

areas which had vegetation floating at the surface. On June 22, 1954, the ratio of the area containing surface vegetation to the area with none was 3:1, while the ratio of numbers of turtles observed was 8:1; the difference is statistically significant (Table 12).

TABLE 12. Chi-square tests for habitat preferences of *Chrysemys*.

Date	Contrasting Situations	Per Cent of Total Area	Number Observed	Number Expected	χ^2	P
June 22, 1954	Aquatic Vegetation Minus <i>Nuphar</i>	75.5	63	53.6	6.81	$P_{99} = 6.63$
	Open Water	24.5	8	17.4		
June 22, 1954	<i>Ranunculus</i>	92.7	39	54.7	61.8	$P_{99} = 6.63$
	<i>Potamogeton foliosus</i>	7.3	20	4.3		
Aug. 13, 1954	<i>Ranunculus</i>	88.4	134	127.3	3.04	$P_{95} = 3.84$
	Filamentous algae	11.6	19	16.7		
June 15, 1957	Filamentous algae	38.6	53	26	45.8	$P_{99} = 6.63$
	<i>Potamogeton foliosus</i>	61.4	14	41		

Chi-square tests were also made to see if *Chrysemys* were distributed at random among several vegetated areas composed of different species of plants (Table 12). On June 22, 1954, more *Chrysemys* were found in beds of *Potamogeton foliosus* than in ones of *Ranunculus longirostris* than could be expected on the basis of a random distribution of animals. However, on August 13, 1954, no difference could be shown in the proportion of animals found in the areas of filamentous algae contrasted to those in the areas of *Ranunculus longirostris*. No other tests could be used to compare the distribution of *Chrysemys* in different areas because the remaining areas were rather small in 1954 and did not contain many turtles. There were significantly more painted turtles observed in areas of filamentous algae than in areas of *Potamogeton foliosus* on June 15, 1957. It is somewhat difficult to interpret the status of filamentous algae. There is a tendency for the algae to occur in shallower water than do the other plants. However, there is no significant difference in the distribution of *Chrysemys* within beds of filamentous algae which are along shore or in the middle of the pond.

During the summer of 1953 the surface of Crane Pond was a mosaic of various plants and open water. The plants reached the surface at different times so that an indication of the preference by turtles for certain vegetation types could be determined by observing the movements of turtles into and out of certain regions as new plant beds developed. By comparing vegetation maps with the distribution of

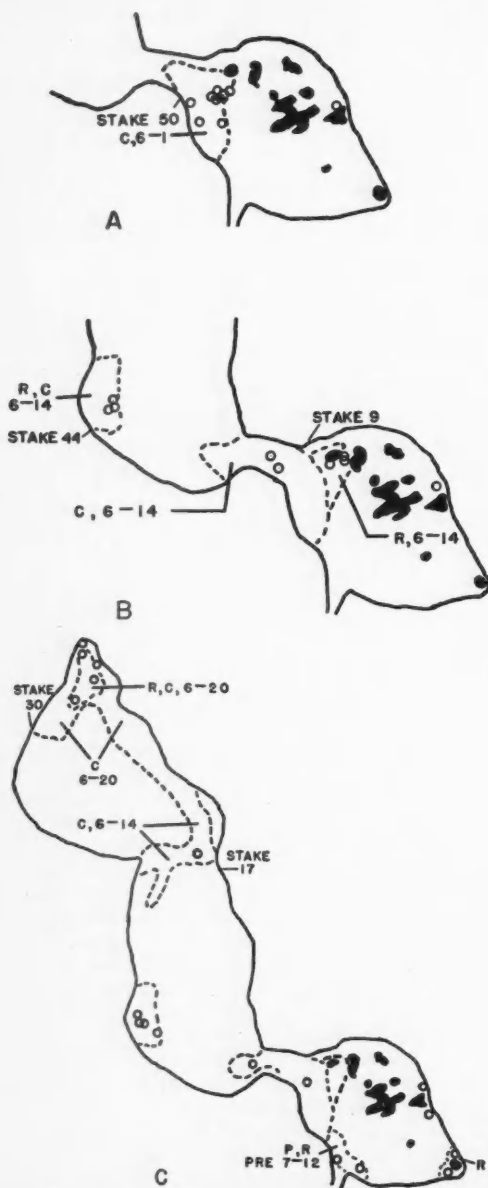


FIG. 7. Distribution of concentrations of *Chrysemys* in relation to the appearance and disappearance of aquatic vegetation at the surface during 1953. Each circle represents an individual animal caught by any method except baited traps. Solid black areas are beds of *Nuphar advena*; areas enclosed by dashed lines are other plant beds. In each notation the letter indicates the plant located in that area as follows: C, *Chara*; R, *Ranunculus longirostris*; P, *Potamogeton foliosus*; RL, rivulariaceous algae. The numbers in each notation refer to the month and day a particular plant bed was first observed at the surface of the water. Compare with Figure 8.

Chrysemys captured by netting and muddling, it was possible to follow the shifts in population centers (Figs. 7, 8).

The vernal distribution of *Chrysemys* during 1953 was centered about four areas, and it is evident that *Typha latifolia* and *Nuphar advena* were the only aquatic vegetation utilized by *Chrysemys* (Fig. 5). About June 1, 1953, *Chara* appeared at the surface in the area off stakes 50-51, and *Chrysemys* quickly moved into the bed (Figure 7, A). At the same time, the turtles abandoned the *Nuphar* which never again was highly utilized that year except occasionally about the periphery. The floating leaves had risen above the water by June 19 so that the plants were emergent. Painted turtles were not common in other parts of the pond at this time.

New clumps of *Chara*, mixed with *Ranunculus*, broke surface off stake 44 about June 14-16, and turtles were evident in this area about June 20 and 21 (Figure 7, B). *Chrysemys* had also moved into an area of *Ranunculus* which had reached the surface off stakes 8-9 (exact date unknown), and they were still present in an extension of the *Chara* bed near stake 50. However, the *Chara* in the area adjoining stakes 50-51 never again attained the number of turtles it had previously contained.

An extensive belt of *Chara* appeared at the surface from stakes 17-30 about June 20. Turtles were found in this area (Fig. 7, C), but largely in those portions of the *Chara* which also contained a high percentage of *Ranunculus*. Scattered patches of *Ranunculus* in the area from stakes 1-4 harbored some turtles. The area of *Ranunculus* and *Chara* (*Ranunculus* became the more abundant) off stake 44 still contained *Chrysemys* in some numbers.

On July 19, *Potamogeton foliosus* was at the surface off stakes 11-14, and turtles soon appeared in this area (Figure 8, D) which had previously been devoid of them. Another area of *P. foliosus* was at the surface by July 12 parallel to stakes 52-53. *Chrysemys* were caught in this area.

The most interesting shift occurred in August of 1953. The belt of *Chara* in the eastern portion of Crane Pond now extended from stakes 17-31 (Fig. 8, E). It had previously been inhabited in numbers by painted turtles only in areas where *Ranunculus* was co-dominant. One species of the algal family Rivulariaceae (probably *Rivularia minutula*, although *Gloeotrichia natans* is also found in Crane Pond), which had been growing adnate to submerged stems and debris, broke loose and floated to the surface. The prevailing westerly winds swept these plants eastward where they became entangled in the *Chara*, especially off stakes 29-31. This accumulation of the rivulariaceous algae in the *Chara* began about August 7. There was also a heavy influx of *Chrysemys* into this area which started no later than August 14 and continued until the end of the month. The floating algae then died, and the *Chrysemys* moved out of the area.

The situation in 1954 was very different, for

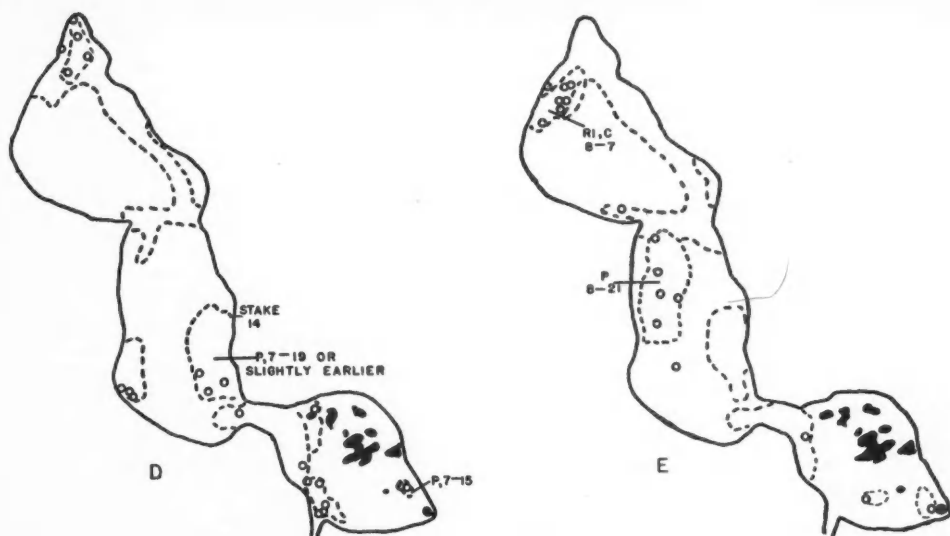


FIG. 8. Distribution of concentrations of *Chrysemys* in relation to the appearance and disappearance of aquatic vegetation at the surface during 1953. Each circle represents an individual animal caught by any method except baited traps. Solid black areas are beds of *Nuphar advena*; areas enclosed by dashed lines are other plant beds. In each notation the letter indicates the plant located in that area as follows: C, *Chara*; R, *Ranunculus longirostris*; P, *Potamogeton foliosus*; R1, *rivulariaceae* algae. The numbers in each notation refer to the month and day a particular plant bed was first observed at the surface of the water. Compare with Figure 7.

Ranunculus was the predominant plant of the entire pond. Hence, this procedure of comparison could not be employed during 1954.

Chrysemys appears to have a hierarchy of preference for certain plant types and conditions within Crane Pond. This is the order of increasing preference: open water, floating *Nuphar advena*, *Chara* sp., *Ranunculus longirostris* (alone or with *Chara* sp.), filamentous algae, *Rivulariaceae* with *Chara* sp., and *Potamogeton foliosus*. *Ranunculus*, filamentous algae and the *rivulariaceae* algae appear about equally favored and are so considered here. *P. foliosus* is probably the preferred plant in this pond, under the conditions observed.

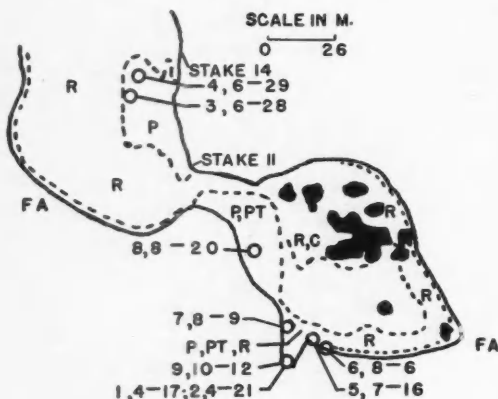
Other aquatic plants which seem to be avoided, at least during the aestival seasons studied are *Potamogeton natans*, *P. amplifolius*, *Typha latifolia*, *Ceratophyllum demersum*, emergent *Nuphar* and *Eleocharis* sp. The *Typha* section of the pond is heavily populated, but this appears to be due to the mats of filamentous algae extending out from the *Typha*. *Potamogeton pectinatus* is probably a preferred plant, but the area covered by this species was too small to determine the place it occupied in the hierarchy.

Responses of individual turtles to vegetation changes. The turtles moving into recently suitable areas of Crane Pond could conceivably come from two sources: animals which emigrated during the spring and have recently returned to the pond, or animals which have been established in the pond some time prior to the appearance of the surface vegetation. Many of the

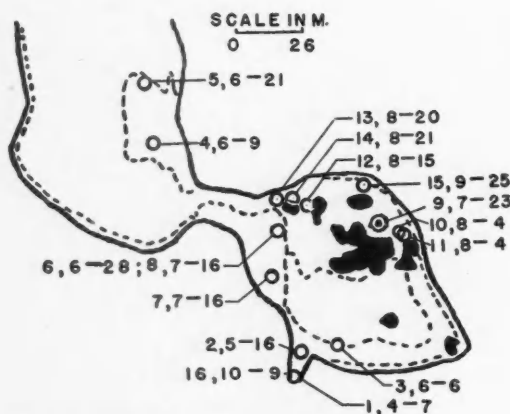
invaders of new masses of aquatic vegetation doubtless are recently arrived immigrants to the pond, but it is known from capture-recapture data that some of the individuals which have previously been resident in a somewhat restricted area will move into newly developed regions. Indeed, if certain types of plants are preferred over others by *Chrysemys*, this behavior would be expected. The stimuli responsible for initiating movement out of one area and into another can be positive or negative in character, or both. Thus, the animal may leave one area because that area lacks a necessary requirement, such as mechanical support, and may restrict the activities to another area which supplies the missing feature.

A bed of *Potamogeton foliosus* reached the surface of the water off stakes 11-14 about May 26, 1954. An unidentified agency destroyed this vegetation after July 8 so that the area was open water by July 18. Figs. 9A and 10C show the successive sites of capture of 2 *Chrysemys* which had been established in the western part of the pond prior to May 26. In June both turtles moved into the *P. foliosus* and surrounding areas. A third *Chrysemys* (Fig. 9B) was also resident in the same area which had been occupied by *P. foliosus*. The turtles shown in Fig. 9 moved into the western section of the pond after the destruction of the *P. foliosus* and did not return to the middle unit; the individual in Fig. 10C remained nearby at least until the middle of July but then took up residence along the shore from stakes 44-48. The shifts in the home ranges, or activity area, of

these animals were correlated with the formation and destruction of certain vegetation units.



A. JUVENILE IN 4TH SEASON



B. FEMALE IN POST-15TH SEASON

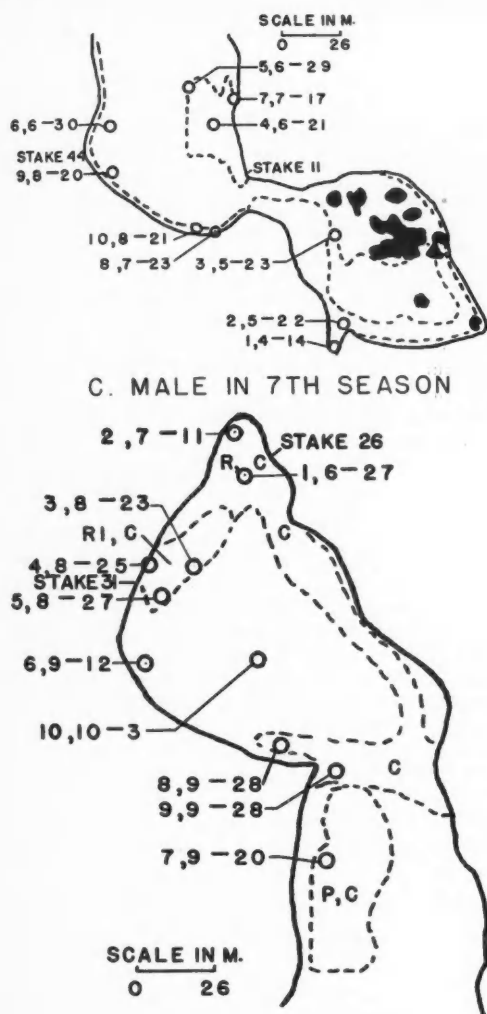
FIG. 9. Locations (circles) of two *Chrysemys* in relation to aquatic vegetation during the aestival season of 1954. Sequences are shown by the first number in the notation; the remaining figures in the notation refer to the month and days of capture. The vegetation types are indicated by letter as follows: C, *Chara*; R, *Ranunculus longirostris*; P, *Potamogeton foliosus*; Rl, rivulariaceous algae.

A slightly different case is presented in Figure 10D. A strip of *Chara* sp. had reached the surface of the water off stakes 29-31 before August, 1953. About August 7, colonies of one of the rivulariaceous algae, which had been attached to submerged stems throughout the pond, floated to the surface and were carried eastward by the wind. The rivulariaceous algae became entangled in the exposed portions of the *Chara* off stakes 29-31 and formed a fairly dense mat there. This condition remained until the

end of August. By late June a painted turtle (Fig. 10D was already established in an area of *Ranunculus* and *Chara* off stake 26, but it moved into the region off stakes 29-31 some time in August although nothing appeared to have changed in the original area. After the disappearance of the rivulariaceous algae this individual moved westward away from the former areas, going into the central section of the pond before returning on or before October 3 to the eastern part. It seems noteworthy that this turtle did not move into the region off stake 30 before the rivulariaceous algae were present even though the *Chara* was already at the surface, and that it left the area after the rivulariaceous algae disappeared although the *Chara* was still present. It is also interesting to note that in the latter part of September it remained in and near a bed of *P. foliosus* which reached the surface about August 21, but which disappeared about October 4. In October it returned to the eastern part of the pond.

It is easy to imagine that animals just returning to Crane Pond encounter these various areas by chance as they move in. Less clear is the method by which resident animals become aware of different areas in Crane Pond other than those in which they are located. Presumably an established animal is somewhat sedentary as long as its requirements are met by its immediate environment. As examples, all the turtles in Figs. 9 and 10 remained in the one area without moving into adjacent areas. When they did leave, they seemed to leave for good, and exodus was correlated with an environmental change. However, my data indicate that *Chrysemys* sometimes makes extralimital journeys. During one 18-day period in mid-summer, a male occupied a small area within the middle part of the pond, left it, moving eastward, and then returned. The shift was evidently not associated with any known vegetational change. This type of movement could indicate that an occupied area lacks some essential, or at least preferred, feature, and the deficiency acts as a stimulus. The response is movement out of that area. If a more favorable site, e.g., one containing necessary support elements, is located, the turtle remains here. If only less favorable areas are encountered, it is conceivable that the turtle would return to the original area or continue wandering until a favorable one was found. In the aestival period it appears that the structure of the vegetation is the feature of the habitat most influential in determining distribution.

The numbers of *Chrysemys* which shift the site of their activities within Crane Pond during the aestival season is not known for certain. Since there is no impartial method for judging whether or not an animal's travels are all within the bounds of a single activity area, an arbitrary standard was used to gain a rough estimate of the number of animals which restrict their activities to one locale throughout the aestival season. There were 22 turtles which were captured 4 or more times during either the



D. JUVENILE IN 1ST SEASON

FIG. 10. Locations (circles) of two *Chrysemys* in relation to aquatic vegetation during the aestival season of 1954. Sequences are shown by the first number in the notation; the remaining numbers refer to the month and day of capture. The vegetation types are indicated by letter as follows: C, *Chara*; R, *Ranunculus longirostris*; P, *Potamogeton foliosus*; RI, rivulariaceae algae.

1953 or the 1954 aestival season. Maps showing the points at which each individual was captured were examined, and the season's movements for each individual were classified as follows: 1) restricted, if the capture points were all within a single homogeneous part of Crane Pond; 2) extralimital, if a single capture outside of a restricted area was preceded and

succeeded by captures within one locale; 3) shifting, if the turtle had been sedentary within one area but had later shifted the site of its activities to another locale. Using this arbitrary classification, approximately 20% of the animals were restricted in their movements, another 20% had extralimital movements, and about 50-60% of the *Chrysemys* had shifting movements.

During the aestival season of 1953, 68 painted turtles were captured 2 or more times within Crane Pond. The minimum direct distance between the most distant points of capture for any one turtle ranged from 3.5 m to 300 m and averaged 89.5 m (the standard error was 15.7 m). Fifty *Chrysemys* were captured two or more times during the 1954 aestival season. The minimum direct distance between the most distant points of capture varied from 6 m to 292 m and averaged 91.2 m (the standard error was 16.7 m).

Features common to plants utilized by Chrysemys. A comparison of features common to the several species of plants which are preferred by *Chrysemys* may reveal factors to which painted turtles respond. The plants most often selected by turtles included *Potamogeton foliosus*, *Ranunculus longirostris*, and filamentous algae of several species. A second group, somewhat less preferred and consisting of *Leersia oryzoides* with *Spirodela polyrrhiza* and *Chara* sp. with rivulariaceae algae, were compared to this first group. The plants of these two groups shared several characteristics. A third lot of plants consisted of unused species and species initially used but later abandoned, such as *Chara* sp., *Ceratophyllum demersum*, *Nuphar advena* and *Typha latifolia*. These plants were compared to the first group to establish outstanding differences.

Other authors have suggested that the structure of the vegetation inhabited by animals is a feature which they select (Beecher 1942), and the plants in Crane Pond were examined with this in mind. Structure in this paper follows the definition of Dansereau (1951): "Structure is the organization in space of the individuals composing a vegetation type or association."

One structural feature common to both used and abandoned plants is the mat of leaves or thalli at the water surface. Turtles avoided areas of open water if otherwise suitable submerged plants were in those same areas, and they also avoided regions in which the plants projected beyond the surface so that no surface mat formed.

The preferred plants possessed one character which was evident when the beds were observed in vertical cross-section. These plant masses could be considered to have a T-structure. The horizontal bar of the T represents the dense mat of terminal leaves floating from the surface downward for about 10 cm, while the vertical bar represents the isolated stems in the otherwise open water beneath the mat. Since the main stems branch out into great masses of leaves distally, there is much greater mass near the surface. This arrangement is modified for filamentous algae,

for most of the filaments are at the surface. Some of the thalli are attached to submerged plants and debris, and others are submerged in shallow water so that a T-structure is attained here also. Actually this vegetation type is better compared to a table, with the top the thick mat of surface vegetation, and the legs the rooted stems.

Another common feature of the structure of the preferred species is the porous nature of the surface mat. The finely dissected leaves of *Ranunculus longirostris*, the ribbon-like leaves of *Potamogeton foliosus*, and the filaments of the algae have little in common individually, but when each species grows in dense aggregations, the floating leaves become entangled to form a mat strong enough to support turtles. However, this mat is composed of so many sub-units that it retains a certain lace-like quality.

Leersia oryzoides, with *Spirodela polyrhiza* entangled in it, forms a modified T and is evidently used by turtles during the vernal season. The graminoid is not emergent at this time, but floats on the surface of the water forming a thin mat composed of linear leaves. *Spirodela* engages in these surface leaves, increasing the cover.

Chara, an abandoned plant, has a cross section which is radically different from the T-structure. The strands of the algae fill most of the space between the bottom and the water surface and resist movement through them. Hence, *Chara* masses tend to be cuboidal and fairly solid. *Nuphar advena*, another abandoned plant, has a T-structure when the leaves float at the surface, but each leaf is a single, large, circular element which contrasts strongly with the leaves of the preferred plants.

Ceratophyllum demersum, generally an abandoned plant during the period of study, is columnar in shape when growing attached to the substrate as it does in Crane Pond. At times this plant forms mats at the surface when the stems are longer than the water is deep. However, the submerged portion of the plants is still quite columnar.

The *Chara*-rivulariaceae algae combination of August, 1953, is more difficult to interpret. Perhaps the rivulariaceae algae on top of the *Chara* forms a modified T-structure although a 2-layered unit would appear to represent the situation better, the upper layer being composed of spheres and the lower layer of a cube of dense *Chara* strands which did not reach the surface. There is also the distinct possibility that the turtles were feeding upon the rivulariaceae plants, but this was never observed.

The plants in Crane Pond tended to grow in pure colonies until there was a drastic change in some environmental feature, generally water level. Whenever this change occurred, it was followed by a rapid increase in the number of plant species found in that area. However, the areas of *Ranunculus* and *Potamogeton foliosus* in which *Chrysemys* were found were quite homogeneous until August. From the latter part of the vernal season until the middle of the aestival season in 1954 the plants found within an area were scaled for sociability on the basis of coverage

(Dansereau 1952). *P. foliosus* increased from 3 (small, well concentrated colonies; local coverage 41-60%) in the spring of 1954 to 5 (pure colonies; local coverage 81-100%) in the summer with only small amounts of *Ranunculus* present. The *P. foliosus* declined and was replaced by many other species, but the area was never again inhabited by *Chrysemys* in any numbers. A typical *Ranunculus longirostris* stand was scaled at 5 by late May, 1954. The *Ranunculus* continued to be dominant throughout the aestival season, but some filamentous algae appeared in the areas of *Ranunculus* by July 4 and *Ceratophyllum demersum* by August 24. The areas of *Ranunculus* continued to be inhabited by *Chrysemys* all summer. *Advantages of the T-structure.* In plants with a T-structure the mat of leaves floating at the surface provides a platform over which all but the largest *Chrysemys* can move. The turtles are not completely out of the water, but at least half of the shell is exposed and the head may be easily extended into the air. At the same time the animal is in water deep enough so that when the head is extended straight forward or depressed, it is beneath the surface. The turtles forage in this position and food may be swallowed easily.

The porous and yielding nature of the mat permits easy access to the surface from beneath and easy egress from the surface to the deeper water so that an alarmed *Chrysemys* may dive quickly through the mat and swim away in the cleared region beneath the mat.

Temperatures taken on August 24, 1954, indicated that the surface temperature of the water in plant beds was within 1°C of the air temperature. However, the water just above the bottom was 3°C to 9°C cooler than the surface water. This reservoir of cool water could provide a shelter during periods of high surface temperatures. In contrast, observations made on September 24, 1954, in a bed of filamentous algae indicate that this warm upper layer may also be advantageous. The temperature of this surface water was 18°C. That of the surface water 6 m distant and in which there was no surface vegetation registered 14.5°C. There was a *Chrysemys* feeding at the time in the filamentous mat. It could easily be that the water surface of the mat may warm up quickly enough during cool periods to permit *Chrysemys* to feed there while nearby areas may be too cool. It was indicated earlier that *Chrysemys* probably begins feeding when the water temperature is about 15°C, so that the importance of this warmer stratum would increase at this critical level.

Perhaps, instead of inhabiting certain plant beds because of structural advantages, painted turtles invade these areas to feed upon these plants in preference to others. Two excellent studies of the feeding habits of *Chrysemys* (Raney & Lachner 1942; Lagler 1943) indicate that this animal is a very generalized feeder. The former paper showed that volumetrically the food was about evenly divided between plant and animal sources, while the latter author found a slight preference for plant material. In any of these

studies it is difficult to separate the plant material eaten *per se* from the plant material accidentally ingested with animal food so that the actual volume of plant food may be slightly less than indicated. At any rate, neither paper shows that *Chrysemys* had a strong predilection for any particular food, plant or animal. Plants found in Crane Pond and vicinity which were mentioned as food were various species of filamentous algae, *Nuphar*, *Potamogeton*, *Najas*, *Spirodela*, *Lemna*, and *Ceratophyllum demersum*. In addition I have sight records of *Chrysemys* eating *Chara* sp. and *Ranunculus longirostris*. The wide variety of food eaten, consisting of plants both favored and unfavored, and many animals, seems to negate the idea that *Chrysemys* seeks certain areas because the plants therein are preferred as food. The method of hunting, to be described later, also precludes this belief.

Distribution within plant beds. It has been shown that *Chrysemys* is inclined to inhabit certain areas more than others, so that their distribution is clumped. It can also be shown that the distribution of painted turtles within a society of one dominant plant species is clumped and not randomized throughout the entire bed even though the vegetation may appear homogeneous. Clark & Evans (1954) have presented a method utilizing distance between nearest neighbors as a measure of the spacing of individuals in a population. Following this technique the distance between nearest neighbors within areas of *Ranunculus* was measured and the R values determined for their distribution on June 22 and August 13, 1954. Clark & Evans state that the value of R will range from 0.0 for complete clumping through 1.0 random distribution to 2.1491 for uniform dispersion. The values obtained for *Chrysemys* (0.4536 and 0.4250, respectively) indicate that the animals were clumped within areas of *Ranunculus*, and the average distance between nearest neighbor was 7.6 m and 3.9 m, respectively. A similar technique could not be employed for other plant beds, for there were not enough turtles in them. The two R values, 0.4536 and 0.4250, are not significantly different, indicating that the population was probably responding similarly at these two different times.

A difficulty in any study of spacing of wild animals is that one does not know how much area an animal or population is occupying. This is especially true if the animals are distributed throughout only one portion of an apparently homogeneous area, as is the case with *Chrysemys* within the areas of *Ranunculus* in Crane Pond. Clark & Evans (1955) have provided a method for determining the distribution of animals which is independent of area. This technique utilizes the percentage of reflexive pairs of individuals, that is, the number of pairs each individual of which is nearer to the other than to any other individual. For randomly distributed populations this percentage is 62.15. The population of turtles in the beds of *Ranunculus* for the June and August census data had 51.3% and 60.5% reflexives, respectively.

This would seem to indicate that although *Chrysemys* is clumped in areas of surface vegetation, and within any one plant bed, the individual turtles exert little social influence upon each other. Thus, individuals appear to be distributed at random in these sub-clumps.

Activities of Chrysemys on mats of floating vegetation. Individuals of *Chrysemys* were commonly observed feeding as they moved over the mats of surface vegetation. Field observations indicated a general similarity in their actions, and a description of the activities of several foraging *Chrysemys* should suffice for a general account of their behavior. A *Chrysemys* in the first season of growth was observed 10:05-10:30 am August 21, 1954, feeding in a patch of filamentous algae over some *Ranunculus longirostris*. The path of this animal was about 11 m in length, and it generally paralleled a 5 m section of the shoreline so that the path turned back on itself. Most of the feeding was done in the areas of filamentous algae, and while the turtle appeared to eat the algae *per se* on one occasion, most of the effort was directed towards obtaining prey. The juvenile moved over or through the upper layers of the mat with the carapace just above the surface. The head was extended forward or slightly depressed so that it was beneath the water when hunting. Most of the time the juvenile nosed about in the vegetation as it moved through it, biting into certain patches. On one occasion the turtle caught some unidentified prey which required about a minute to crush and swallow. Another time it disturbed some animal which darted off, with the turtle following for 5-10 cm before capturing it. A third capture required 15-20 seconds of chewing. The *Chrysemys* passed a small stick which projected about 3 cm above the surface of the water. As it passed beneath this stick, the turtle struck perfunctorily at it, missed, and continued on. This seems to epitomize the hunting technique employed upon most occasions: exploratory strikes of the head into vegetation to disturb potential prey sufficiently to make it move, then active pursuit.

When a *Chrysemys* saw some prey at a distance every effort was made to capture it. A juvenile was seen to move rapidly over the surface of the vegetation in an unsuccessful attempt to capture an odonate resting on the vegetation. On June 22, 1955, a large male painted turtle was observed beneath the surface in an area of fairly open water as it swam towards a transforming *Rana catesbeiana* floating on the surface. The frog jumped away when the turtle was still 20-30 cm distant. The *Chrysemys* persisted in following it into a patch of *Potamogeton foliosus*, where it attempted to approach from beneath. After two more attempts to capture the turtle gave up the chase. On the same day a large female *Chrysemys* was observed hunting frogs in a similar fashion. The turtle was at the surface and evidently saw a small *R. catesbeiana* about 30 cm ahead of it in some *Chara* sp. The turtle swam beneath the surface to within 5-10 cm of the frog, but the frog leaped away. The *Chrysemys* surfaced, saw the frog again, and tried to

catch it in the same way. The ranid again eluded the turtle and disappeared.

The following is another fairly typical example of feeding activities of *Chrysemys* that also describes the behavior of painted turtles when they come to undesirable areas. This turtle, a juvenile in the third season of growth, was observed from 11:20 am until 12 noon on August 9, 1954. The animal was originally feeding in *Ranunculus*, moving at, or just beneath, the surface with the carapace partly exposed at times and covered at others. Its head remained beneath the water except when the animal breathed or watched me. Movement through the vegetation was fairly steady but interspersed with frequent short rests, a minute being the longest time taken. At times the juvenile appeared to eat only the *Ranunculus*, especially old, brownish pieces. Even when feeding on this the turtle continued to move about. At other times it seemed to be searching for, and biting at, unidentified prey with rapid thrusts of the head. Initially the turtle was located in a bed of *Ranunculus longirostris*, but it soon entered an area of open water, a space 1 m in diameter. The *Chrysemys* swam through this area quickly, returning to the *Ranunculus*. It continued moving through the *Ranunculus* until it came to the margin of a *Nuphar* bed. The turtle started to enter the *Nuphar* but then returned abruptly to the *Ranunculus*. Finally the animal came to the open water at the edge of the *Ranunculus*, then it turned back into the *Ranunculus*, in spite of the fact that I was now in front of the animal. The juvenile continued in my direction, moving through the *Ranunculus* until it became wary and entered some nearby *Nuphar*. During the entire period of observation the animal seemed to avoid areas which are less favored by *Chrysemys*, i.e., open water and *Nuphar*.

On other occasions it was observed that a *Chrysemys*, moving across open water from one patch of vegetation to another, generally would swim well beneath the surface of the open water and frequently just above the submerged vegetation. If the distance across these areas of open water was not too great, the animal did not come up until it attained surface vegetation. *Chrysemys* were also seen swimming just beneath the mat of surface vegetation. At times they would remain there after they had become alarmed.

Return of Chrysemys to activity areas of former years. It has been shown that some *Chrysemys* move from one area to another during the aestival season of one year and that other turtles will remain within relatively restricted areas for the entire season. There is also some evidence that some turtles will remain within, or will return to, the same general area in successive aestival seasons but that other *Chrysemys* will not inhabit the same general area in two successive summers. The extent of this voluntary return to areas formerly occupied was determined on the basis of the mapped aestival capture points of 33 *Chrysemys* collected during the summers of 1953 and 1954.

It was arbitrarily decided that for each animal the activity area of one of the two seasons must be represented by at least two captures while the area of the other season must be indicated by one or more captures. In those instances in which the animal was caught more than twice, the activity area was represented by a closed figure made by drawing a continuous line through the fewest number of points so that all of the capture points were on the line or within the closed figure. Where only two capture points were recorded, the area was represented by a circle whose diameter was the distance between the two points and whose center was the midpoint between them. Single points of capture remained as such. If, for an individual turtle, any portion of one bound figure intercepted the figure representing the area occupied during the other summer, or if a bound figure contained the single point of capture of the other season, the two activity areas were considered to be coincident.

On the basis of the above criteria, 43% of the turtles returned, at least for a short period, to the same activity area occupied in 1953. The remaining 57% did not return to the same area occupied the preceding year. Actually, only 13% of the animals restricted their aestival activities to more-or-less the same area during the two summers.

THE AUTUMNAL SEASON

The autumnal season, extending from September 1 until the formation of the permanent ice cover, is one of thermal extremes. During 1953 the air temperature varied from a maximum of 33°C to a minimum of -10°C. The air temperature dropped below 0°C before September 15, 1953, and then fluctuated considerably. It reached a second maximum of 29°C before it dropped to -10°C at the end of November. The water temperature ranged from a high of 27°C to a low of 0°C during the fall of 1953. The permanent ice cover formed on December 13, 1953 and on December 1, 1954. Some painted turtles were active until December 6, 1953 and November 20, 1954.

Some of the activities of the turtles during the first month of the fall differ from those of the remaining part of the autumnal season. During most of September the animals continue to eat, but they do not do so later in the autumnal season. On September 20, 1953 a *Chrysemys* was observed feeding in a patch of filamentous algae. The water temperature was 22°C. On the same day another painted turtle captured and partly devoured a *Rana catesbeiana* 5.3 cm in snout-vent length. The latest date on which a *Chrysemys* was observed hunting for food was on September 24, 1954 when two turtles were active in a bed of aquatic vegetation. The temperature of the surface water was 18°C while that of the water beneath the mat was 13°C. The insulation of the upper stratum of water from the lower, colder one by the vegetation mat provides a volume of water which can be warmed sufficiently during the day to enable *Chrysemys* to feed until late in the season. Since

Chrysemys feeds lethargically at temperatures of 15°C and below, the presence of a warm upper stratum of water is undoubtedly an additional factor in influencing the animals to move into or to remain within areas of surface vegetation.

Although the painted turtles continue to eat during the first three or four weeks of September, they cease growing by late August.

The spatial distribution and movements of the painted turtles during the autumnal season differ according to the height of the water levels of the various bodies of water during the fall. During a dry autumnal season the turtles concentrate in Crane Pond; during a wet season those animals which have immigrated into Crane Pond will emigrate out to the surrounding swamps and marshes.

During 1953 only 26.1 in of precipitation were recorded at the George Reserve weather station for the entire year. Neither Southwest Swamp nor Fishhook Marsh retained standing water during that fall although the substrate remained moist in areas. The only active *Chrysemys* observed were in Crane Pond. The behavior of the animals within Crane Pond was still strongly influenced by the location of certain plants, but the effects of the wind blowing over the water came to play an increasingly important role in influencing the distribution of the turtles. The effect of the wind and of the concomitant temperature changes was demonstrated on September 27, 1954, when the distribution of the turtles visible in two areas of the eastern part of Crane Pond was correlated with variations in certain environmental factors (Table 13). Light, water temperature on the

TABLE 13. Grouping of *Chrysemys* in two contiguous areas with certain contrasting environmental features. East end of Crane Pond on September 27, 1954.

Variants	Sector A	Sector B
Percentage of Total Area.....	44.7	55.3
Number of <i>Chrysemys</i>	45	5
Wind Velocity in Ft/Min.....	130	430
Light in Foot Candles.....	6000	6000
Temperature of Surface Water in <i>Ranunculus</i> in °C.....	22.0	17.0
Temperature of Water 30 cm below Surface in <i>Ranunculus</i> in °C.....	14.4	14.4

bottom beneath the mats of vegetation, relative amounts of open water and areas containing *Ranunculus* were similar in the two areas. Area A was well protected from the westerly wind by a peninsula which projected out into the water at stake 38 (Fig. 2), but area B was subject to the full force of the wind. The wind velocities of the two areas were 130 ft/min, and 430 ft/min, respectively. The temperature of the surface water was higher in area A than in area B, 22°C to 17°C, for the strong winds over B

probably mixed the warm upper water with the deeper, cooler water. The portion of B which was least inhabited by *Chrysemys* at the time of this survey was the site of a dense concentration of *Chrysemys* during the aestival season. This was also the area most exposed to the wind on September 27. Thus, the preference for A, or the avoidance of B, is correlated with the relative exposure of these two areas to the westerly winds and to the difference in the temperature of the surface water.

The distances moved by the animals during the autumnal season of 1953 were greater than the distances moved during the aestival season. The minimum distance between the points of capture most distant from each other varied from 0 to 336 m and averaged 130 m for the 54 *Chrysemys* captured 2 or more times during the autumnal season. Since many turtles emigrated during the fall of 1954, comparable estimates of the extent of movements were not obtained for that year.

Field observations indicated a general movement by *Chrysemys* resident in Crane Pond from regions of shallow water into regions of deeper water as the weather became cool, and animals were relatively more abundant in the eastern deeper part of the pond during the fall, prevernal and early vernal seasons than in the middle and western sections. Evidently, for hibernation, painted turtles move into areas which are more stable thermally. As a check upon these field observations the pond was subdivided into 3 units, and the positions of successive captures of individual turtles were followed to see if there was any directional trend in movement from the aestival to the autumnal season (Table 14). The 3 subunits consisted of the eastern, middle and western parts of the pond as defined by the major natural constrictions of the perimeter.

TABLE 14. Changes in location of *Chrysemys* within Crane Pond from the aestival season to the fall. The sub-ponds refer to the natural sections of the pond which are formed by the indentations of the shoreline (Fig. 1).

Location in aestival season	Number of individuals	Position of <i>Chrysemys</i> in the fall relative to that in the aestival season		
		Percentage showing no change	Percentage moving westward	Percentage moving eastward
1953				
East sub-pond.....	19	73.7	26.3
Middle sub-pond.....	14	35.7	28.6	35.7
West sub-pond.....	32	28.1	71.9
1954				
East sub-pond.....	7	100.0	0.0
Middle sub-pond.....	8	38.0	50.0	12.0
West sub-pond.....	9	77.8	22.2

During the fall of 1953 the maximum depths in the eastern, middle, and western units were 24 in (61.0 cm), 12 in (30.5 cm), and 18 in (45.7 cm), respectively. However, most of the eastern section varied from 12-24 in, the middle from 6-12 in, and the western from 6-18 in.

About three-quarters of the animals caught in the eastern unit during the aestival season of 1953 remained in the same area during the fall. One third of the turtles captured in the middle section remained there, but the other two thirds which moved out were about equally divided between those moving eastward and those moving westward. In the fall there was a very striking shift (72%) eastward of those *Chrysemys* which had formerly been captured in the western part of the pond.

Precipitation was much greater during 1954, and consequently the water level was higher. This seemed to stabilize the distribution of those turtles which did not emigrate in the fall. There was no movement out of the eastern unit, and only reduced movement out of the western section in the fall of 1954. However, the turtles from the middle unit left that area, most going westward. The depth of all units in the pond was about 18 in greater than that of the previous fall. Animals which emigrated through the inlet during that season in 1954 are not included in Table 14.

In 1954, 40.8 in of precipitation were recorded at the George Reserve weather station, and, while there was no flow of water between Crane Pond and the surrounding bodies of water during the aestival season, these latter areas did contain some water throughout the summer. Rainfall, totaling 8.5 in, flooded all of the basins during October, and water began to flow into Crane Pond from the west. This influx of water was followed by an emigration of *Chrysemys* (Table 15).

TABLE 15. The numbers of *Chrysemys* emigrating through the inlet to Crane Pond during the autumn of 1954.

Date	Number Emigrating	Date	Number Emigrating
October		November	
3.....	1	7.....	4
9.....	4	10.....	1
10.....	1	11.....	3
11.....	9	13.....	1
12.....	63	17.....	2
13.....	31	18.....	2
14.....	16	19.....	11
19.....	1		
22.....	6		
23.....	11		
24.....	7		
25.....	2		

The autumnal emigration is very similar to the vernal ones. The peak in the number of animals emigrating is rapidly reached in both cases (Tables 4 and 15), and most of the animals exit via the inlet (Table 3). The percentage composition of the different classes of turtles seems to be similar to the composition of the animals emigrating during the spring of 1954 and 1955 when substantial numbers of emigrants were captured. During the fall approximately 19.9% of the emigrants through the inlet were juve-

niles, 30.1% were subadult females, 24.4% were adult females and 25.6% were adult males (Table 5). The sex ratio among all the sexually mature autumnal emigrants was 0.85 ♀♀/1.0♂. This ratio is somewhat lower than that observed during the vernal emigrations, 1.0 ♀♀/1.0♂ in 1954 and in 1955, but it is higher than the ratio observed for adult animals in the entire population. This latter ratio is 0.76 ♀♀/1.0♂. One difference between the emigrating turtles of the vernal and autumnal seasons is that the juveniles emigrate relatively early in the fall as contrasted to their time of emigration in the spring (Table 6).

The diel pattern of movement through the inlet was generally the same during the two seasons. In the fall (Table 8) the greatest rate of emigration occurred about noon and shortly thereafter. The temperature of the water flowing through the inlet was more variable than the temperature of water at stations within Crane Pond, just as in the vernal season. In addition, there was little movement out of Crane Pond on those days when the inlet temperature did not exceed that of the pond.

The surface vegetation within Crane Pond became inundated with the influx of water into the pond during the fall of 1954. Taking the depth of water in Crane Pond on August 23 as an arbitrary standard with a value of 0 cm, the increase in depth can be followed through the course of the emigration. On October 8 the depth of the water had increased to 3.5 cm. On October 10 it was 8.0 cm. Emigration started in full on October 11. By October 15 the depth of the water had increased to 20.3 cm, and it remained at that level until May, 1955. This increase in the depth of the water in Crane Pond covered many of the beds of surface vegetation so that the mat no longer floated on top of the water. In addition, the heavy rains also beat the vegetation down. The end result was that the surface of the pond, while it still contained some surface vegetation appeared somewhat like Crane Pond during the spring before the plants attained the surface in late May.

The autumnal emigration indicates that the phenomenon of emigration is not limited temporally to the spring and that, if the proper constellation of factors are present, it may occur at any time. The autumnal emigration also suggests rather strongly that the exodus is not under the influence of some seasonal factor, such as increasing length of daylight, which is mediated through the endocrine system.

DISCUSSION

The distances moved by *Chrysemys* during any season seem to follow certain patterns (Table 16). The average distance traversed during the prevernal season is relatively constant, 41 m for 5 turtles in 1953 and 45 m for 7 turtles in 1954. Admittedly, the samples are small, but they tend to bare out the general observations in the field. There is also little variation in distance traversed during the aestival season. The average distance between farthest points of capture of individual turtles was 89.5 m for 68 turtles in 1953, 91.2 m for 50 animals in 1954, and

TABLE 16. The extent of the spatial movements of the painted turtles, *Chrysemys picta marginata*, caught two or more times during any one of the annual seasons. The distances refer to the minimum direct distance over water between the two most distant points of capture for each individual animal.

Season and year	Number of animals captured	Range of minimum distance in m	Average minimum distance in m	Standard error in m	Length of season in days	Average time between first and last capture in days	Comments
Prevernal 1954....	5	3.4-124	41	21 days + 16 days with ice cover	12.4	Data collected before emigration
Prevernal 1955....	7	9.2-92.3	45	20	1.4	Data collected before emigration
Vernal 1953.....	9	0.0-301	144	46	13.1	Data collected after emigration
Vernal 1954.....	8	1.0-279	63	46	2.5	Data collected after emigration
Aestival 1953.....	68	3.5-300	89.5	15.7	92	28.5	—
Aestival 1954.....	50	6.0-292	91.2	16.7	92	30.3	—
Aestival 1957.....	7	6 -276	85.8	92	32.1	—
Autumnal 1953....	54	0 -336	130.0	21.8	104	29.7	No emigration
Autumnal 1954....	10	11 -306	88.1	92	15.9	Emigration

85.5 m for 7 *Chrysemys* in 1957. The data for the vernal and autumnal seasons are more variable. In the vernal season of 1953, 9 *Chrysemys* traversed an average distance of 144 m while in 1954, 8 traveled an average of 63 m. The limited samples and the difference in the average lengths of time between first and last captures, 13.1 days and 2.5 days makes it difficult to interpret the discrepancy in distance. A similar discrepancy prevails in the fall. Fifty-four *Chrysemys* moved an average of 130 m during the autumnal season of 1953, but 10 moved only 88.1 m during the same period in 1954. The fact that many *Chrysemys* emigrated in the fall of 1954 and not in 1953 undoubtedly accounts for the discrepancy in average distance and time observed for the two years. Of course, there is more variation in various environmental factors during these latter two seasons than in the prevernal and aestival seasons. For instance, during the prevernal seasons there are never any plants at the surface, and there are always some present during the aestival. In contrast, some plants may rise to the surface during the late vernal season (as in 1954) or may disappear during the fall rains (as in 1954). In addition, the water level remains high during the prevernal season, is constantly dropping during the summer, but fluctuates during the spring and fall.

Although the painted turtles inhabiting Crane Pond move from one area to another between seasons or within a single season, some populations of *Chrysemys* observed for various lengths of time by other workers appear to be more sedentary. Pearse (1923) studied the *Chrysemys* inhabiting an area of 547 acres located behind a sand bar in a bay of Lake Mendota, Wisconsin. The turtles were netted, individually marked and released. One hundred sixty-six turtles were recaptured during the course of the investigation between 1917 and 1921, and of these 30% had moved away from the initial point of capture and 70% had not. Pearse concluded that "... painted turtles are rather sedentary animals, and, if their en-

vironment remains favorable, will remain in one locality for years." Lake Mendota is probably a much more stable habitat than Crane Pond.

Cagle (1944) concluded on the basis of homing experiments and by following the movements of marked *Chrysemys* in Illinois and Michigan that painted turtles (as well as other species) inhabit a particular area to which they will return if released elsewhere. The data for this conclusion concerning *Chrysemys* are rather sketchy since there were few areas suitable for *Chrysemys* in the vicinity. Cagle recognized that the return of the painted turtles to these areas should not be construed as unqualified evidence for homing. He also found that some species of turtles including *Chrysemys* make seasonal movements away from the home ranges during each spring and late fall.

Cahn (1937) mentioned observing *Chrysemys picta marginata* in Illinois on land during the summer and fall and stated that their movements had no connection with age, sex, breeding, or hibernation.

Williams (1952) observed the movements of painted turtles at Fish Lake in southeastern Michigan, and his data show that some painted turtles return to their home range after removal from it. However, Williams neglects to mention that most of the areas in which he collected were the best turtle habitats in the lake. The present author is aware of this fact because he collected turtles at Fish Lake on several occasions himself. It is not surprising that the *Chrysemys* returned to those areas. Williams found that other *Chrysemys* wandered about the lake and had no apparent home range.

The overall conclusion to be drawn from the work of these four investigators who studied *Chrysemys picta marginata* is that individuals of this subspecies may or may not restrict their activities to limited areas.

It is now essential to provide an integrated view of the factors determining the spatial and temporal distribution of the painted turtle as represented by

the Crane Pond population. The importance of certain factors, such as the need for water for a semi-aquatic organism, will not assume large proportion in the following scheme. This is not because such factors are trivial, but because they are so essential to the physiology of the animals that it is understood automatically that they figure large in determining the distribution of painted turtles. The following discussion assumes that sufficient water is present to support a population of *Chrysemys*.

The factors most constantly associated with shifts in location by *Chrysemys* is the presence or absence of vegetation or other structures which can support the animals in the water. The spring emigration occurs before the plants have attained the surface in Crane Pond, and the fall emigration occurs only when autumn rains raise the water level to such a degree as to inundate the mats of vegetation. During the aestival season the turtles in Crane Pond are practically confined to those areas occupied by certain species of plants. Typically these plants are those which have a thick mat of vegetation floating at the surface with stems rising from the substrate to the mat. Shifts in activity areas of *Chrysemys* can be correlated with the disappearance of some plant beds or the appearance of others. All in all, it may be concluded that the structure of the plant beds, their organization in space, is of overwhelming importance in determining the distribution of *Chrysemys*. The possible role of vegetation will be discussed shortly.

It is first necessary to stress that factors other than vegetation can and do influence the behavior of *Chrysemys*. Among these factors are currents, such as that flowing into Crane Pond through the inlet, and the temperature gradients of such currents. Other investigators suggest that the behavior and movements of turtles in general are influenced by other factors. Parker (1922) found that young loggerhead turtles (*Caretta caretta*) moved towards an open horizon and away from interrupted ones. Since *Chrysemys* can distinguish between lines which differ as little as 1 mm in width (Casteel 1911), it is certainly conceivable that the painted turtles can orient themselves in relation to the hills north and south of Crane Pond and to the lower points to the east and west. Noble & Braslovsky (1935) showed that hatchling *Chrysemys picta* and *Chelydra serpentina* can detect light reflected from water surfaces even if they cannot see the water. *Terrapene carolina* can orient by using the sun (Gould 1957).

It is possible that past experience is important in influencing the behavior of *Chrysemys*. Casteel (1911) and Tinklepaugh (1932) demonstrated learning in *Chrysemys*, and the experience of emigrating or of shifting activity ranges could modify activities in successive periods.

Although the factors affecting the shifts in location of *Chrysemys* have been tentatively identified, it is essential to present a conceptualization of the interaction of such extrinsic factors with intrinsic ones as a basis for explaining the movements of the painted turtles in the Crane Pond area. The overall behav-

ioral pattern is composed of appetitive and consummatory acts (Tinbergen 1951).

Turtles, as secondarily semi-aquatic animals, need physical support to remain at the water surface. This support is offered by the water and by aquatic plants (or partially submerged rocks, stumps, etc.), or by a combination of the two. It is clear from the evidence provided in this paper that turtles will concentrate in areas having surface vegetation. Here they can crawl about at the surface of the floating mats. They can obtain air easily, yet are in water so that they can swallow their food. Turtles on top of the surface mat are exposed to the sun, and the insolation of the water surface by the mat from the cold water provides an area thermally favorable for eating in cool weather. Contrariwise, the cooler depths beneath the mat can serve as refugia during torrid weather.

The behavior of a *Chrysemys* supported by these mats of surface vegetation differs considerably from one in water containing no surface vegetation. The supported turtles move over the mat surface half submerged, half emerged, snapping at and into various clumps of vegetation as they feed. Air is readily available for breathing, and the animal is in the water it needs to swallow its food. Some turtles remain relatively motionless, evidently sunning in the shallow water. In contrast, *Chrysemys* in deep open water rarely swim at the surface but dive down and swim just above the substrate or above the submerged vegetation. They generally move directly to areas of surface vegetation.

This difference in behavior suggests that the complete lack of support by plants or the wrong type of support plants induces a form of appetitive behavior in which the animal moves from place to place until presented with a stimulus which releases a consummatory act or acts, generally those alluded to above. The nature of consummatory and appetitive acts have been discussed by Tinbergen (1951). This stimulus is of a general nature in contrast to the specific releasers identified in consummatory acts of a social nature. The T-structure mats of plants, or partly submerged logs, would be examples of such generalized releasers. Such mats of many plant species, *Ranunculus longirostris*, *Potamogeton foliosus*, filamentous algae, all induced the consummatory acts, and the turtles in such plant beds would remain within restricted areas until the character of the area changed.

As is well known, field studies of most vertebrates, especially those dealing with birds and mammals, indicate that the young animals have a greater tendency to wander than do mature adults. That the opposite is true in painted turtles is evident from the observations of Williams (1952) and from the present study. Williams found in his homing studies of the painted turtle that the larger turtles did not return to the site of their original capture as readily as did the smaller ones. It was observed in the Crane Pond study that there was a greater tendency for the adults to emigrate than for the young animals to do so. This odd exception can be explained on the basis of the present interpretation of *Chrysemys* behavior by as-

suming that the heavier animals need structural support more than do the lighter ones and that the threshold at which the consummatory behavioral pattern of traveling is elicited is lower in the large animals than in the small ones.

During the emigrations of the vernal and autumnal seasons this variable, appetitive, searching pattern is secondarily influenced by other factors—thermal gradients, water currents, and topography to name a few. The overall result is that animals' movements are oriented rather than random.

The final conclusion is that the stability of the activity range of painted turtles is dependent upon a wide variety of factors. Under the relatively unstable conditions of Crane Pond, the turtles frequently shift the location of their activities, and while their travels are all confined to the area from Southwest Swamp to the eastern end of the Ditch, it is impossible to say that this entire area constitutes the activity range of a single animal. Under more stable conditions, as is presumed to be the case in Pearse's study, the activity ranges of the animals are restricted to very limited areas.

SUMMARY

1. A population of approximately 1000 individuals of the painted turtle *Chrysemys picta marginata* Agassiz was studied in and around Crane Pond on the Edwin S. George Reserve near Pinckney, Michigan.

2. Turtles were captured by various methods. The following data were recorded: identification number, sex, date, time, location. The turtles were released at the point of capture as soon as possible.

3. The annual activity cycle of *Chrysemys* was described on the basis of seasonal differences in behavior. The following were the seasons studied: pre-vernal, vernal, aestival, and autumnal.

4. The prevernal season, March 15 to March 25, was the period during which *Chrysemys* came out of hibernation. There was little activity at this time.

5. The vernal season, extending from March 26 to May 31, is the period in which *Chrysemys* emigrates from Crane Pond to outlying bodies of water. The migration occurs only during periods of high water, most of the animals leaving the pond through the inlet. One of the main factors orienting emigration through the inlet appears to be the temperature regimen of the inlet. More adults emigrate and more juveniles remain in the pond than would be expected on the basis of chance. There is a tendency for more adult females to emigrate than males. Turtles which remained in Crane Pond during the vernal season became concentrated about the four available sunning spots.

6. The aestival season extends from June 1 to August 31. During this season the vernal emigrants gradually filter back into Crane Pond and become concentrated in areas in which the vegetation reaches, but does not project, beyond the surface. The preferred vegetation has a structure in the form of a

T with thick mats of leaves or thalli representing the horizontal bar. The plants with this structure are: *Potamogeton foliosus*, *Ranunculus longirostris*, and various species of filamentous algae. The turtles move about as such types appear or disappear. It was shown that the distribution of *Chrysemys* was clumped even within a bed of one particular plant species. The activity area of individual painted turtles was not restricted to one locale. During any one season, *Chrysemys* may or may not return to areas inhabited during similar seasons of previous years.

7. The autumnal season extends from September 1 until December 1. It is not as well characterized as the other seasons. The animals tend to move into areas of deeper water. Emigration may also occur at this season under the proper conditions.

8. Other authors have concluded that *Chrysemys* is rather sedentary. The fluid nature of the movements of the turtles in the Crane Pond area suggests that this species is readily adaptable to varying conditions.

9. The lack of suitable vegetation induces an appetitive behavioral pattern in which the turtles move about until they come to an area containing the proper vegetation type.

LITERATURE CITED

- Beecher, W. J. 1942. Nesting birds and the vegetation substrate. Chicago: Chicago Ornithological Society.
- Breckenridge, W. J. 1955. Observations on the life history of the soft-shelled turtle *Trionyx ferox*, with especial reference to growth. Copeia: 5-9.
- Breder, R. B. 1927. Turtle trailing: a new technique for studying the life habits of certain testudinata. Zoologica 9: 231-243.
- Cagle, F. R. 1944. Home range, homing behavior and migration in turtles. Misc. Publ. Mus. Zool. Univ. Mich. 61: 1-34.
- . 1950. The life history of the slider turtle, *Pseudemys scripta troostii* (Holbrook). Ecol. Monog. 20: 31-54.
- Cahn, A. R. 1937. The turtles of Illinois. Ill. Biol. Monog. 16: 1-218.
- Carr, A. & D. K. Caldwell. 1956. The ecology and migrations of sea turtles. I. Results of field work in Florida, 1955. Amer. Mus. Nov. No. 1793: 1-23.
- Carr, A. & Leonard Giovannoli. 1957. The ecology and migrations of sea turtles, II. Results of field work in Costa Rica, 1955. Amer. Mus. Nov. No. 1835: 1-32.
- Casteel, D. B. 1911. The discriminative ability of the painted turtle. Jour. Animal Behavior 1: 1-28.
- Clark, P. J. & F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35: 445-453.
- . 1955. On some aspects of spatial pattern in biological populations. Science 121: 397-398.
- Dansereau, P. 1951. Description and recording of vegetation upon a structural basis. Ecology 32: 172-229.
- . 1952. The varieties of evolutionary opportunity. Rev. Canad. de Biol. 11: 305-88.

- Gould, E. 1957. Orientation in box turtles, *Terrapene c. carolina* (Linnaeus). Biol. Bull. 112: 336-348.
- Heape, W. 1932. Emigration, migration, and nomadism. Cambridge: W. Heffer and Sons Ltd. 369 pp.
- Lagler, K. F. 1943. Food habits and economic relations of the turtles of Michigan with special reference to fish management. Amer. Midland Nat. 29: 257-312.
- Legler, J. 1954. Nesting habits of the western painted turtle, *Chrysemys picta bellii* (Gray). Herpetologica 10: 137-144.
- Nichols, J. T. 1939. Range and homing of individual box turtles. Copeia: 125-127.
- Noble, G. K. & A. Braslovsky. 1935. The sensory mechanism involved in the migration of newly hatched fresh-water turtles. Anat. Rec. (suppl.) 64: 88.
- Parker, G. H. 1922. The crawling of young loggerheads toward the sea. Jour. Exp. Zool. 36: 323-331.
- Pearse, A. S. 1923. The abundance and migration of turtles. Ecology 4: 24-28.
- Raney, E. C. & E. A. Lachner. 1942. Summer food of *Chrysemys picta marginata* in Chautauqua Lake, New York. Copeia: 83-85.
- Sexton, O. J. 1957. Notes concerning turtle hatchlings. Copeia: 229-230.
- Stickel, L. F. 1950. Populations and home range relationships of the box turtle, *Terrapene c. carolina* (Linnaeus). Ecol. Monog. 20: 351-378.
- Tinbergen, N. 1951. The Study of Instinct. Oxford: Clarendon Press. 228 pp.
- Tinklepaugh, O. L. 1932. Maze learning of a turtle. Jour. Comp. Psychol. 13: 201-206.
- Williams, J. E. 1952. Homing behavior of the painted turtle and musk turtle in a lake. Copeia: 76-82.
- Woodbury, A. M. & R. Hardy. 1948. Studies of the desert tortoise, *Gopherus agassizi*. Ecol. Monog. 18: 145-200.

AN ANALYSIS OF A POPULATION OF SNOWSHOE HARES IN NORTHWESTERN MONTANA

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INTRODUCTION

The snowshoe hare (*Lepus americanus*) has long been an object of particular interest because of its marked variations in population numbers from time to time. Such natural fluctuations intrigue the wildlife ecologists because they afford an opportunity to study naturally varying populations. Studies under these conditions offer opportunities to understand the factors in nature which affect and control population levels and to compare them with factors which may be artificially applied.

The present study was undertaken with the general, long-range objective of trying to analyze the natural causes of fluctuations in snowshoe hare populations. The plan is to study as many aspects of the hare's ecology as possible on an island which has an isolated population. This report deals with three specific topics in the general field of hare ecology: a technique for estimating hare numbers by sampling the fecal pellets in the area; factors of the physical environment which affect hare distribution and abundance; and life history of the hares as revealed by livetrapping and field observations.

I am indebted to Dr. David E. Davis, Division of Vertebrate Ecology, School of Hygiene and Public Health, Johns Hopkins University, who supervised the research and the thesis on which this paper is based; to Mr. Paul Hickie, Acting Chief, Branch of

Wildlife Research, U. S. Fish and Wildlife Service, under whose administration the project was conducted; to Drs. Carl L. Larson, J. Frederick Bell, Glen M. Kohls, C. M. Eklund and Messrs. Nick Kramis and John Moore, U. S. Public Health Service Laboratory, Hamilton, Montana, for assistance with studies of disease and parasites and with photography; to Drs. Gordon B. Castle, P. L. Wright and LeRoy Harvey of the Flathead Biological Station of Montana State University for the use of Station facilities; and to Mr. A. L. Roe, Center Leader, and his staff at the Missoula Research Center of the Intermountain Forest and Range Experiment Station for their continuing close cooperation. I wish also to thank, for their help with the field operations, the many residents of the Flathead Lake area. Especially Mr. Art Ellithorpe, Mr. and Mrs. Floyd Bucher and Jack Bucher, Mrs. J. C. Phillips, Mr. and Mrs. Walter Staves and Homer Staves, Mr. and Mrs. Ike Lattin, Mrs. Minnie Smith, Mr. and Mrs. C. G. Fry, Mr. and Mrs. Vern Fast and the late Lon Fast, and Mrs. Helen Harris.

STUDY AREA

Field studies were conducted in the Flathead Region of northwestern Montana, principally on Bull Island in Flathead Lake. In this area hares are relatively abundant and many types of habitat are avail-

able, some good and some entirely unsuitable for hares. The large irregularly-shaped expanse of the lake and the varied topography around it present conditions such that many small "islands" of habitat occur. These are isolated from similar habitats either by water, as in the case of the true islands in the lake, or by ecological variations as in the case of wooded mountains or hills surrounded by grasslands. Such isolated tracts of hare habitat offer many opportunities for controlled observation and experimentation.

Geology. The study area lies adjacent to and includes parts of three mountain ranges of the Rocky Mountain system, and an intermediate valley. The Flathead valley lies between the Mission and Selish Ranges. Flathead Lake is about 2,900 ft above sea level. Much of the geologic character of the study area results from the forces of glaciation. Flathead Lake was formed largely as a result of a large moraine which dammed the valley.

Flathead Valley has an hour-glass shape, broad throughout the northern and southern thirds of its length and narrow in the central third. Flathead fills the entire bottom of this narrow central section. At the narrowest point, the Lake is nearly constricted in two and here a peninsula (Finley Point) and a string of islands form a girdle across the lake (Fig. 1). The largest of these islands in The Narrows is Bull Island, the center of the hare studies.

CLIMATE

The Flathead Lake region lies on the west flank of the Rocky Mountains, exposed to the influences of the winds from the Pacific Ocean and partly protected by the mountains from the cold arctic air masses that move down the east side of the continental divide in winter.

At Flathead Lake the average annual precipitation is about 18 in (Fig. 2). There is a well marked wet season in May and June when there is more than two inches of rainfall per month. A less pronounced wet season occurs in late fall and early winter when the normal precipitation is just over 1.5 in per month, part of it in the form of snow. Dry seasons occur in February and March and in July and August when the normal precipitation is about 1.0 in per month.

Bull Island is the largest of five islands which lie in a line across The Narrows in Flathead Lake. It is 100 acres in size, about three-fourths of a mile long from north to south and about one-third mile wide. Its contours result from the geologic forces which left a long slope to the east and a more precipitous short drop to the west. The highest point is about 160 ft above the lake surface.

VEGETATION

In this description of the plant ecology of Bull Island the ecological concepts of Daubenmire (1952, 1953) and the plant nomenclature of R. J. Davis (1952) are followed.



FIG. 1. Looking eastward across The Narrows at Flathead Lake, Montana. In the background is the Mission Range. The white snowcapped peaks of the Swan Range are glimpsed above the Mission Range. The long strip of land in front of the Mission Range is Finley Point. The five islands of The Narrows appear next reading down the picture. First is a small unnamed island. Next is tiny Burnt Island. Then Bull Island, the largest of the five. Below Bull Island is little Bull Island, and next to it another unnamed island. In the foreground is the West Shore. Ice-filled Quarry Bay lies in the right foreground.

Bull Island lies in an area in which the Douglas fir (*Pseudotsuga taxifolia*) zone predominates. But the climate tends to be on the more xeric side of the norm for this association so that a strong tendency toward a zone of Western yellow pine (*Pinus ponderosa*) occurs on the drier sites.

On the north and east slopes Douglas fir forms the tree union (Fig. 3). The understory is primarily a snowberry (*Symphoricarpus albus*) union including a liberal admixture of ninebark (*Physocarpus malvaceus*) (Figs. 3, 4). This community is therefore referred to as the Douglas fir/Ninebark association.

Mature yellow pine trees occur as a seral component in the Douglas fir/Ninebark association. On the south and west slopes the pine becomes more and more dominant and the Douglas fir almost disappears (Figs. 3, 5). There is little pine reproduction in this pine stand. Only one small area, less than one acre in size has an abundance of small sapling reproduction. Possibly this indicates an approach to the upper margin of a Yellow pine/Wheatgrass (*Agropyron spicatum*) association. More likely this pine-inhabited area represents one of the long-standing

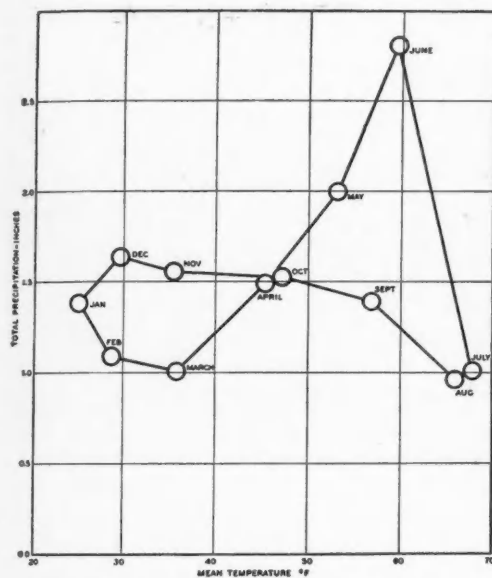


FIG. 2. Hythergraph for Bull Island, Flathead Lake Montana. The values for temperature and precipitation represent the average normal values for the two weather stations nearest the Island, one at Polson five miles to the south, and one at East Shore ten miles to the northeast (Anon. 1952, Anon. 1953).

several stages in the Douglas fir succession such as Daubenmire describes (in Davis 1952).

Several local variations in vegetation exist within the associations mentioned. Around the shoreline there is a narrow zone of moist open sites. Wherever soil is deep enough black cottonwood (*Populus trichocarpa*) and quaking aspen (*P. tremuloides*) grow. Choke cherry (*Prunus virginianus* var. *demissa*) and Rocky Mountain juniper (*Juniperus scopulorum*) are also more abundant along the shoreline than elsewhere.

At the north end of the island there is a small, compact stand of western larch (*Larix occidentalis*) within the Douglas fir/Ninebark association.

Near the center of the east side of the island is an old clearing which was made about 45 years ago and then allowed to revegetate naturally. Here Douglas fir reproduction forms clumps interspersed among open areas which bear forbs, grasses and sparse shrubs.

Douglas fir reproduction of practically all ages occurs in clumps irregularly over the island wherever there are openings among the mature trees. One such clump in the southwest corner of the island is noteworthy because of its large size, about 13 acres, and the density of the vegetation. The trees are often so crowded together that nearly all ground vegetation, except mosses, has been shaded out (Figs. 3, 6).

For the Douglas fir/Ninebark association the shrub species were listed according to presence or absence on 262 1/10,000-acre plots mechanically spaced at

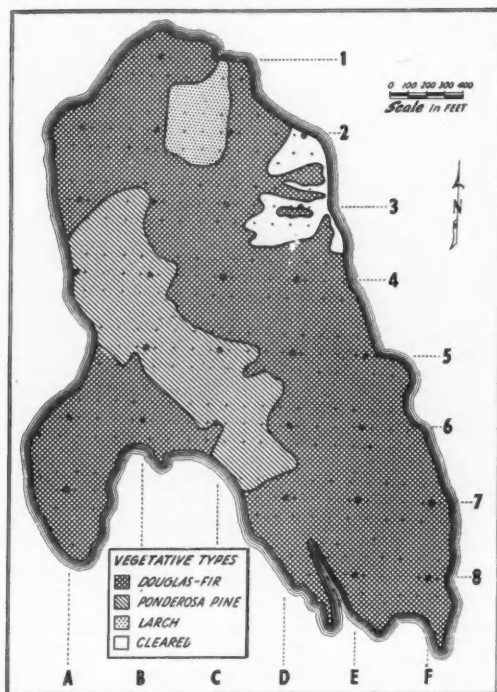


FIG. 3. Type map of the tree unions on Bull Island, Flathead Lake, Montana. The numbers 1-8 and letters A-F are symbols related to the live-trap grid. The circled dots are live-trap sites. Other dots mark the locations of the 1/10,000-acre plots.



FIG. 4. Douglas fir/Ninebark association typical of the north and east portions of Bull Island, Flathead Lake, Montana.

100-ft intervals (Fig. 3). Some idea of the relative abundance of the various species is obtained from the tally of plots on which they occurred (Table 1). Snowberry occurred on 56% of the plots, creeping hollygrape (*Berberis repens*) on 30%, etc. Only 14% of the plots bore no shrubs. Two shrubs, syringa



FIG. 5. Yellow pine/Wheatgrass association, south- and west-facing slopes of Bull Island, Flathead Lake, Montana. Outstanding ground cover is balsam-root.



FIG. 6. Dense stand of Douglas fir saplings and poles on the flat southwest part of Bull Island, Flathead Lake, Montana.

TABLE 1. Occurrence of shrubs on 262 quadrats, each 1/10,000 acre, Bull Island, Flathead Lake, Montana.

Species	Per cent of Plots
Snowberry, <i>Symphoricarpos albus</i>	56
Creeping Hollygrape, <i>Berberis repens</i>	30
White Spiraea, <i>Spiraea betulifolia</i>	24
Ninebark, <i>Physocarpus malvaceus</i>	18
Kinnikinnick, <i>Arctostaphylos uva-ursi</i>	9
Ocean Spray, <i>Holodiscus discolor</i>	6
Rose, <i>Rosa</i> sp.....	3
Service Berry, <i>Amelanchier alnifolia</i>	3
Gooseberry, <i>Ribes cereum</i>	2
Choke Cherry, <i>Prunus virginianus</i> var. <i>demissa</i>	1
Willow, <i>Salix</i> sp.....	1
Squaw Currant, <i>Ribes cereum</i>	T ¹
Orange Honeysuckle, <i>Lonicera ciliosa</i>	T
Syringa, <i>Philadelphus Lewisii</i>	T
Mountain Maple, <i>Acer glabrus</i>	T
Plots with no shrubs.....	14

¹ T—trace

(*Philadelphus lewisii*) and mountain maple (*Acer glabrus*), grow sparsely in the area, but did not occur in the plot sample.

Beneath the pine trees in the pine stand there are but few shrubs (Fig. 5). Occasionally creeping hollygrape invades this xeric association and rarely snowberry and spiraea (*Spiraea betulifolia*) occur there. Mostly, the understory is composed of grasses and forbs. Rough fescue (*Festuca scabrella*) is the dominant grass, balsamroot (*Balsamorhiza* sp.) the dominant forb.

MAMMALS

Dice (1923) has reported upon the mammal associations and habitats of the Flathead Lake region. Current information on mammals has been obtained from field observations, trapping and reports of local residents. Following is an annotated list of the mammals occurring on the island that may be of signifi-

cance to the snowshoe hare population. The nomenclature follows that of Burt & Grossenheider (1952).

Mink (*Mustela vison*). Occurred commonly on Bull Island although probably none of them in residence there very long at a time.

Striped Skunk (*Mephitis mephitis*). Only one record: adult skunk caught in a rabbit trap set at 6A.

Badger (*Taxidea taxus*). Partly decomposed carcass seen August 6, 1953, at south end of island. On August 4, 1953, one seen running over rock outcrop near southeast end of island. Several times during late summer saw results of badger digging at the bases of rotted stumps. On September 4, 1953 badger visited camp. Evidence of badger abundance indicates not more than one or two individuals on the island. No evidence of possible movement onto or off the island.

Red Fox (*Vulpes fulva*). Mr. Art Ellithorpe reports trapping two on Little Bull Island two years before present study began.

Red Squirrel (*Tamiasciurus hudsonicus*). Douglas fir and yellow pine forest afford good habitat on Bull Island. Squirrels are present there in relatively large numbers.

Deer Mouse (*Peromyscus maniculatus*). Observed frequently in camp at night in summer of 1953. Droppings plentiful at Harris cabin, one of three cabins on the island.

Longtail Vole (*Microtus longicaudus*). Fairly abundant. Occasionally seen at trap sites. Frequently visit hare traps to feed on the bait leaving accumulations of droppings.

Mule Deer (*Odocoileus hemionus*). Present on island in summer but possibly not in winter. Six does and fawns and two bucks separately identified on island in summer, 1953. May have been more.

Whitetail Deer (*Odocoileus virginianus*). A few—apparently three or four—on island at all times. Ap-

parently both species of deer swim back and forth at will from mainland.

Six mammals which could be expected to occur on Bull Island are not there. They are ground squirrels (*Citellus columbianus*), chipmunks (*Eutamias* sp.), pocket gophers (*Thomomys talpoides*), coyotes (*Canis latrans*), beaver (*Castor canadensis*) and bobcats (*Lynx rufus*). All of these occur on the adjacent mainland in habitats which are represented on the island.

The island is seldom visited by humans. It is divided among four owners. The only property regularly used is the Fry cabin which is used for summer vacations only. Rarely casual visitors stop at the island for a picnic or excursion.

BIRDS

Only one of the birds of Bull Island appears to be directly concerned with the ecology of the snowshoe hares. This is the great horned owl (*Bubo virginianus*). Its role as a predator on hares will be discussed in detail later.

Three other raptors, red-tailed hawk (*Buteo borealis*), bald eagle (*Haliaeetus leucocephalus*), and osprey (*Pandion haliaetus*) have been seen on the island. The red-tailed hawk was seen but once in the 17 months of the study and is therefore considered of no appreciable significance in the island's ecology. The bald eagle is a common resident which nests on the island. However, it lives on birds and fish and there is no evidence that it preys on any of the island's mammals. Similarly the osprey, a summer resident, lives largely on fish.

There are a few resident American magpies (*Pica pica*) on the island. These may prey upon young hares or other small mammals, but no evidence of such activity is at hand.

METHODS OF STUDY

Two general methods were used in the study of the hares on Bull Island—live trapping and direct field observations.

LIVE TRAPPING

Twenty-nine live traps were used. They were the Havahart wire mesh traps about 1 ft square and 4 ft long, opening at both ends (Fig. 7). These were set in a grid pattern over the entire island at 400-ft (122 m) intervals (Fig. 3). The trap was set at the most likely-looking trap site within a 50-ft radius of the intersection. Grid intersections were designated by a system of numbers and letters. Grid lines running east and west were numbered 1 to 8. The lines running north and south were lettered A to E. Each of the 24 intersections and their corresponding trap sites were designated with a combination of one number and one letter each, e.g. 2B, 8E, etc.

Traps were first set on February 10, 1953. The grid had not been surveyed at that time and the traps were placed at random. Only 6 traps were then in use. On March 16, 1953, the entire grid had been surveyed and 26 traps were set at intersections. On

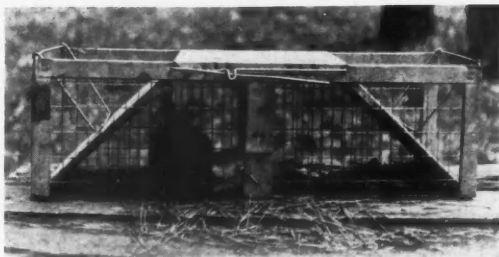


Fig. 7. The Havahart trap used in trapping hares. A snowshoe hare is shown with ear tags and colored discs in the ears.

June 8 three traps were added to complete the full complement of 29 traps, one at each grid intersection. Thereafter trapping followed the standard grid pattern except for occasional variations which will be noted whenever important.

Traps were set once or twice each month for periods of about four successive nights. Between trapping sessions the traps were sprung and left in place.

Several kinds of bait were used—apples, carrots, parsnips, dandelions, Douglas fir twigs and alfalfa hay. Most of these attracted the hares successfully, but the hay was finally used as the "standard" bait, because it was easy to obtain and store, was effective at all seasons of the year, and was fairly selective in attracting only hares. Deer and long-tailed voles were attracted to the hay and occasionally tripped the traps, but not often enough to hamper the study unduly.

A standardized field record form was developed on which to record live-trapping data. Space was provided to record the following data. General information: date; number and location of traps set; traps tripped (agent). Information on captured hares: location, sex, weight, ear tag numbers and colors, ear length, hind foot length, testes size and position, embryos (number and size), lactation, suckling, pelage color, ringworm symptoms, ticks.

When each hare was first captured it was equipped with a set of ear tags (Fig. 7). A tag consisted of an aluminum "cotter key" with a flat head bearing a distinctive number, and two plastic colored washers. Most of the hares were tagged in both ears. A few were tagged in only one ear. In referring to individual hares the number stamped on only one tag is used, e.g. 309 designates the hare with tag number 309 in the left ear and number 310 in the right ear. The colored markers were round discs $\frac{3}{4}$ inch in diameter cut from plastic sheets. They served to identify the animals seen in the field and mechanically as a bearing surface for the bent ends of the aluminum tag. With several different colors and the two-ear combinations it was possible to distinguish all individuals by color combinations.

Very few tags were lost from the ears. The greatest loss occurred in the live traps where the wire of the trap occasionally slipped between the disc and

the ear tearing out the entire tag assembly and at times a piece of the ear. When this occurred the tag was simply replaced at once and no loss of identity occurred. Once a hare appeared in a trap with a healed wound in one ear indicating that a tag had been lost outside a trap. The individual was identified by the tag in the opposite ear. On another occasion a tag-assembly was picked up at a dust bath where a hare had lost it. I believe that in spite of these rare unilateral losses no hare's identity was lost after it was first tagged.

DIRECT FIELD OBSERVATIONS

Two types of field observations were made—systematic surveys of vegetation and pellet plots, and casual observations which were the day-to-day observations made incidentally to other field work. The latter were recorded under various species accounts in the same field notebook that contained the systematic records. They covered such matters as food habits, predation, habitat relationships, daily activities, range and the like and are presented under the various headings of these topics.

The systematic observations were concerned mostly with sample plot studies, particularly with regard to pellet census technique and vegetative cover. These studies are described later. The sample plots are 1/10,000-acre plots marked by an iron spike at the center. The plots were systematically distributed over the island as shown in Fig. 3.

CENSUS TECHNIQUE

Counts of fecal entities have been used as indices to the abundance of cattle, deer, cottontail rabbits and jackrabbits. MacLulich (1937) used the pellet count for snowshoe hares. The method has two outstanding advantages—it is less costly than many other census methods, and it permits analysis of population by habitat or other subdivisions of the range. The pellet method is especially valuable for extensive studies where information is needed only on population levels. Where detailed life-history studies are in progress, live-trapping data collected in line with the study provides census information.

In the following analysis of the pellet-census technique two questions are of prime importance: Does the number of pellets vary as the number of animals varies on the area? What is the numerical relationship between the number of pellets and the number of hares? To answer these questions, information is needed on variations in pellet numbers and concurrently on variations in hare numbers. From these two statistics hare-pellet calibrations can be computed. Although this is essentially a simple problem in correlation analysis, there are several practical complications.

First, it is impossible to know precisely how many hares are present at a given moment. Any estimate of hare numbers is only as good as the census methods currently available. The accuracy of these methods is largely unknown at present. Second, the number of pellets in an area can only be estimated through

sampling. Presumably this estimate has a high degree of accuracy, since the pellets are stationary and provide a manageable population from which an unbiased sample can be selected. Therefore this difficulty is not insurmountable. However, a third obstacle is introduced by the fact that the sampling procedure for pellets is laborious and cannot always be accomplished synchronously with the hare census. Thus we are often working with hare data taken at one time and pellet data at another time. For these reasons one must work with averaged trend relationships instead of simple regression components.

In the following account the hare census computations are presented first, followed by the pellet-sampling procedures, and finally the relationship between the two is described. Hare numbers were computed from live-trapping data. Computations were of two kinds—the recapture method and the calendar-graph method. For the recapture method the hares marked in one trapping period were used as the pre-marked animals to be sampled in the next trapping period. The calendar-graph method consists of plotting horizontal lines across a graph, the abscissa of which is marked off by calendar periods. One line is entered for each animal live-trapped. The line starts at the date of the first capture and terminates at the date of last capture. The number of animals known to be present at any given date is determined by erecting a perpendicular at the point on the abscissa represented by that date. The number of horizontal lines intercepted by the perpendicular line is the number of animals known to be present.

Data for the calendar graphs are presented in tabular form, the adults of 1953 in Tables 2 (females) and 3 (males), and immature hares of 1953 in Tables 4 (females) and 5 (males). The dates when each hare was captured are shown as X's in the columns corresponding to the trapping periods shown at the tops of the tables.

In Tables 2 and 3 (adults) the lines are extrapolated to the left to February 11, 1953, the beginning date of the study. This extrapolation is justified by the fact that, although some hares were first captured at later dates than others, all of them were present from the beginning of the study. This assertion is based on the assumption that a hare which was an adult in 1953 must have been present since the preceding breeding season in 1952, or longer, and therefore was present at the start of the studies. The fact that the study was located on an island where immigration is unlikely provides the logical basis for this assumption.

In Tables 4 and 5 (immature hares of 1953) a similar extrapolation prior to the first capture is possible. Here the extrapolation is extended to the estimated time of birth. The time of birth is estimated with the aid of the growth curve described later in the section on development. The weight of the hare at the time of the first capture is used as the point of entry on the ordinate of the growth graph. The age of the hare is then read opposite the point of intersection of the age-growth curve.

TABLE 2. Data for the calendar graph of the adult female snowshoe hares of 1953. The X's indicate those periods when the hares were captured. The entries on each line terminate at the period when hares were last captured.

[illegible]

TABLE 3. Data for the calendar graph of the adult male snowshoe hares of 1953. The X's indicate those periods when the hares were captured. The entries on each line terminate at the period when hares were last captured.

[illegible]

TABLE 4. Data for the calendar graph of female snowshoe hares born in 1953. The dashed lines start at the estimated time of birth. The X's indicate those periods when the hares were captured. The entries on each line terminate at the period when hares were last captured.

Tag No.	Estimated Date of Birth	Estimated Date When Pellet Production Begins	DATES STUDY AREA WAS TRAPPED																						
			1953															1954							June 10-30, 1955
			Apr. 14-17	Apr. 28-May 1	May 13-15	May 25-28	June 9-12	June 17-19	June 23-24	July 7-10	July 21-23	July 28-31	Aug. 12-14	Aug. 20-28	Sept. 22-25	Oct. 16-20	Nov. 8-11	Nov. 28-Dec. 1	Jan. 5-8	Jan. 29-Feb. 2	Mar. 3-6	Mar. 31-Apr. 3	May 21-25	July 13-16	
80	Apr. 15	May 25	-	-	X	X	X	X	-	-	-	X	X	X	-	X	X	X	-	-	-	-	-	-	
94	Apr. 5	May 15	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
213	Apr. 18	May 27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
217	May 3	June 12	-	-	-	-	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
219	May 8	June 17	-	-	-	-	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
221	Apr. 25	June 4	-	-	-	-	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
236	May 21	June 30	-	-	-	-	X	X	X	X	-	-	-	-	-	-	X	X	-	-	-	-	-	-	
238	May 28	July 7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
244	Apr. 26	June 5	-	-	-	-	X	X	X	X	-	-	-	-	-	-	X	-	-	-	-	X	X	-	
250	May 31	July 10	-	-	-	-	X	X	X	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-	
253	Apr. 11	May 21	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
255	May 26	July 5	-	-	-	-	-	X	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	
257	Apr. 23	June 2	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
259	June 7	July 17	-	-	-	-	-	-	X	-	-	-	X	X	X	-	-	-	-	-	-	-	-	-	
261	May 28	July 7	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
273	June 9	July 19	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
275	May 27	July 6	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	
277	May 10	June 19	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	
291	July 8	Aug. 17	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	
295	June 7	July 17	-	-	-	-	-	-	-	-	X	X	X	X	X	-	-	-	-	-	-	-	-	-	
101	Apr. 10	May 20	-	-	-	-	-	-	-	-	-	X	X	X	X	-	-	-	-	-	-	-	-	-	
103	June 1	July 11	-	-	-	-	-	-	-	-	-	X	X	X	X	-	-	-	-	-	-	-	-	-	
105	July 16	Aug. 25	-	-	-	-	-	-	-	-	-	X	X	X	X	-	-	-	-	-	-	-	-	-	
107	Apr. 28	June 7	-	-	-	-	-	-	-	-	-	X	X	X	X	-	-	-	-	-	-	-	-	-	
125	June 5	July 15	-	-	-	-	-	-	-	-	-	X	X	X	-	X	X	X	-	X	-	X	X	-	
129	July 14	Aug. 24	-	-	-	-	-	-	-	-	-	X	X	X	X	-	-	-	-	-	-	-	-	-	
133	July 20	Aug. 29	-	-	-	-	-	-	-	-	-	X	X	X	X	-	-	-	-	-	-	-	-	-	
137	July 18	Aug. 27	-	-	-	-	-	-	-	-	-	X	X	X	X	-	-	-	-	-	-	-	-	-	
139	July 16	Aug. 25	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	
141	Apr. 16	May 26	-	-	-	-	-	-	-	-	-	-	-	X	X	-	X	X	-	-	-	-	-	-	
*	July 24	Sept. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
149	Apr. 10	May 20	-	-	-	-	-	-	-	-	-	-	-	X	X	X	-	-	-	-	-	-	-	-	
151	Apr. 10	May 20	-	-	-	-	-	-	-	-	-	-	-	X	X	X	-	-	-	-	-	-	-	-	
157	June 28	Aug. 7	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	
161	May 14	June 22	-	-	-	-	-	-	-	-	-	-	-	X	X	X	-	-	-	-	-	-	-	-	
169	June 30	Aug. 9	-	-	-	-	-	-	-	-	-	-	-	X	-	-	X	X	X	X	-	-	-	-	
177	July 23	Sept. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
179	July 23	Sept. 1	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	
191	July 25	Sept. 3	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	
195	July 15	Aug. 24	-	-	-	-	-	-	-	-	-	-	-	-	X	X	X	X	-	-	-	-	-	-	
199	Apr. 10	May 20	-	-	-	-	-	-	-	-	-	-	-	X	X	X	-	X	X	-	X	-	-	-	
303	July 3	Aug. 12	-	-	-	-	-	-	-	-	-	-	-	-	X	X	X	-	-	-	-	-	-	-	

* No tag.

This age at first capture is then extrapolated to the left on the calendar graph to the date of birth, shown in the second column in Tables 4 and 5. These estimates of birth-dates are only approximate, since the actual growth curve for this population is not known. Furthermore, the curve represents an estimated *average* weight-at-age relationship and therefore each extrapolated value is subject to errors of sampling variation.

Since calibrations are to be made with pellet counts, the life lines should begin to enter the tallies at that point where the hares concerned could be ex-

pected to be producing fecal pellets on the pellet plots. It is not known at what age this occurs, but it is probably after the young are weaned and start to depend exclusively on foraging for their livelihood. Weaning occurred in Severaid's (1942) captive hares usually at about 25-28 days, although terminal litters nursed longer—up to 56 days. At 28 days the Bull Island hares weighed 300 gm on the average (see weight-age chart, Fig. 8).

Another indication of the proper age at which to terminate the pre-trapping extrapolations may be the average age-weight at which hares are first caught,

TABLE 5. Data for the calendar graph of male snowshoe hares born in 1953. The dashed lines start at the estimated time of birth. The X's indicate those periods when the hares were captured. The entries on each line terminate at the period when hares were last captured.

Tag No.	Estimated Date of Birth	Estimated Date when Pellet Production Begins	DATES STUDY AREA WAS TRAPPED																	
			1953										1954							
			Mar. 29-Apr. 2	Apr. 14-17	Apr. 28-May 1	May 13-15	May 25-28	June 9-12	June 17-19	June 23-24	July 7-10	July 21-23	July 28-31	Aug. 12-14	Aug. 20-28	Sept. 22-25	Oct. 16-20	Nov. 8-11	Nov. 28-Dec. 1	Jan. 5-8
			Apr. 29-May 1	May 13-15	May 25-28	June 9-12	June 17-19	June 23-24	July 7-10	July 21-23	July 28-31	Aug. 12-14	Aug. 20-28	Sept. 22-25	Oct. 16-20	Nov. 8-11	Nov. 28-Dec. 1	Jan. 5-8	Jan. 29-Feb. 2	Mar. 3-6
99	Apr. 16	May 26	-	-	-	-	X	-	-	-	-	-	-	-	-	X	-	-	-	-
205	Apr. 30	June 9	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-
209	Apr. 23	June 2	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-
215	Apr. 15	May 25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
223	May 26	July 5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
227	May 1	June 10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
230	Apr. 17	May 27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
240	May 5	June 14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
242	Apr. 23	June 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
246	Apr. 9	May 19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
248	May 29	July 8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
263	May 13	June 22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
265	Apr. 15	May 25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
267	June 14	July 24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
269	June 30	Aug. 9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
271	June 6	July 16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
279	May 24	July 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
281	July 8	Aug. 17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
283	May 17	June 26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
285	May 25	July 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
287	May 21	June 30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
289	July 12	Aug. 21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
297	July 2	Aug. 11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
109	July 20	Aug. 29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
111	May 28	July 7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
113	June 8	July 18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
115	June 8	July 18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
117	June 20	July 30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
119	May 29	July 8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
121	May 13	June 22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
123	July 13	Aug. 22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
127	June 29	Aug. 8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
131	July 18	Aug. 27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
135	Apr. 24	June 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
143	June 12	July 22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
145	Apr. 1	May 11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
147	July 21	Aug. 30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
155	July 4	Aug. 11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
159	July 2	Aug. 11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
163	June 26	Aug. 5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
165	July 2	Aug. 11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
167	June 23	Aug. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
171	May 28	July 7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
173	May 28	July 7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
175	June 21	July 31	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
181	Apr. 10	May 20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
183	June 10	July 20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
185	July 14	Aug. 23	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
189	July 12	Aug. 21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
193	June 15	July 25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
197	June 18	July 28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
301	July 25	Sept. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
305	Apr. 10	May 20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
*	Aug. 27	Oct. 6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
307	July 3	Aug. 13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
309	Sept. 6	Oct. 16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

* No tag.

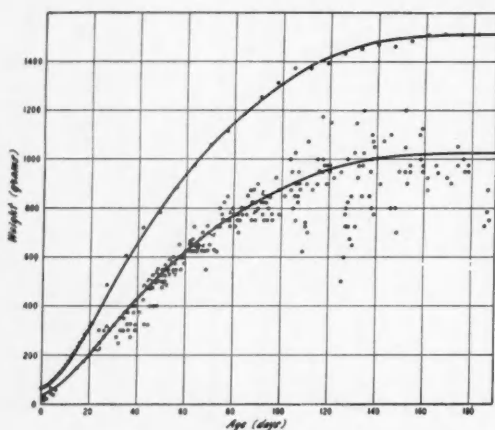


FIG. 8. Growth curves for weights of snowshoe hares. The upper curve is drawn from Severaid's (1942) data. The lower curve is adapted from Severaid's curve to fit the mean weights of Montana hares. Open dots represent weights of hares studied as described in the text.

for they may be presumed to be trapped at a rate corresponding to the extent of their foraging activities and hence to the extent of pellet production on the plots. The mean weight at first capture for the young of the 1953 class was 551 gm for the males and 514 gm for the females (Table 6). Since the

TABLE 6. Weight at first capture of male and female snowshoe hares born in 1953.

Weight Class (Grams)	Females (No.)	Males (No.)
0- 99	0	0
100- 199	2	4
200- 299	6	5
300- 399	10	4
400- 499	3	6
500- 599	7	12
600- 699	6	8
700- 799	0	8
800- 899	3	3
900- 999	1	1
1000-1099	1	2
1100-1199	3	1
Total	42	54
Mean Weight	526	551
Conf. Lim. (.95)	88.8	62.2

mean weights of the two sexes are not significantly different, they are combined to give a mean weight for all of 540 gm. This corresponds to an age of 53 days (Fig. 8).

Probably the proper date at which the extrapolations should be terminated lies somewhere between the 28th day (when weaned) and the 53rd day (when first trapped). Lacking any objective criteria for further refinement of the proper termination-date, it is arbitrarily taken as the mid-point between the

28th and 53rd day of age, namely age 40 days. These dates are indicated in the third columns of Tables 4 and 5.

The results of the two types of population analysis, the calendar-graph and the recapture, are shown in the graph for the adults (born before 1953) (Fig. 9, lower part) and for hares born in 1953 (Fig. 9, middle).

The upper graph (Fig. 9, upper) shows the estimates of the total population—both adults and the young of 1953. For the calendar-graph estimates the upper graph is a simple total of the other two. For the recapture estimates the values in the upper graph are new calculations based on the summed data for adults and immature hares.

The calendar-graph method underestimates the true population. The graph for adults (Fig. 9, lower) shows that it took from February 12 to August 24, 1953 to fill the complement of trapped adults. During that time adults were dying and it is likely that some of them died before they were trapped. Such individuals would not be registered on the calendar graph. Similar bias affects the estimations of numbers of immature hares, for it is likely that some of these young hares also grew to a size to qualify for the record, but then died without being captured.

A further bias occurs in the calendar-graph method in the practice of terminating the life lines at the date of last capture. Obviously the hares lived beyond the dates of their last capture and their life lines should be extended and tallied accordingly.

In all three graphs of Fig. 9 the calendar-graph curve has a special downward bias at the terminal portion of the curve. This results from the fact that when trapping ceases, there is no further opportunity to re-capture animals, and therefore those life lines which would have been extended, are dropped one or a few at a time beginning at some indefinite trap-period prior to the terminal date.

All of these sources of bias depress the estimate. Since there is no sound method of correcting for them, it must be recognized that the estimates reported here are lower than the actual population.

The estimates made by the calendar-graph method can be compared with those made by the recapture method. The recapture estimates for both adults and immature hares tended to be as low as those of the calendar-graph. Apparently the recapture method also underestimates the population, perhaps even more than the calendar-graph technique. This may be a result of "trap habit" in some individuals (e.g. No. 11, Table 2) which become addicted to entering traps, a condition which introduces a depressing bias in the estimate of the population.

Recapture estimates were computed for the immature hares and the total hares only for the period after August, 1953. Prior to that time (and even in August and September) the recapture method was not valid because appreciable recruitment was occurring. Use of the recapture at times when recruitment is occurring results in inflated estimates. This effect is demonstrated in the August estimates (111 for

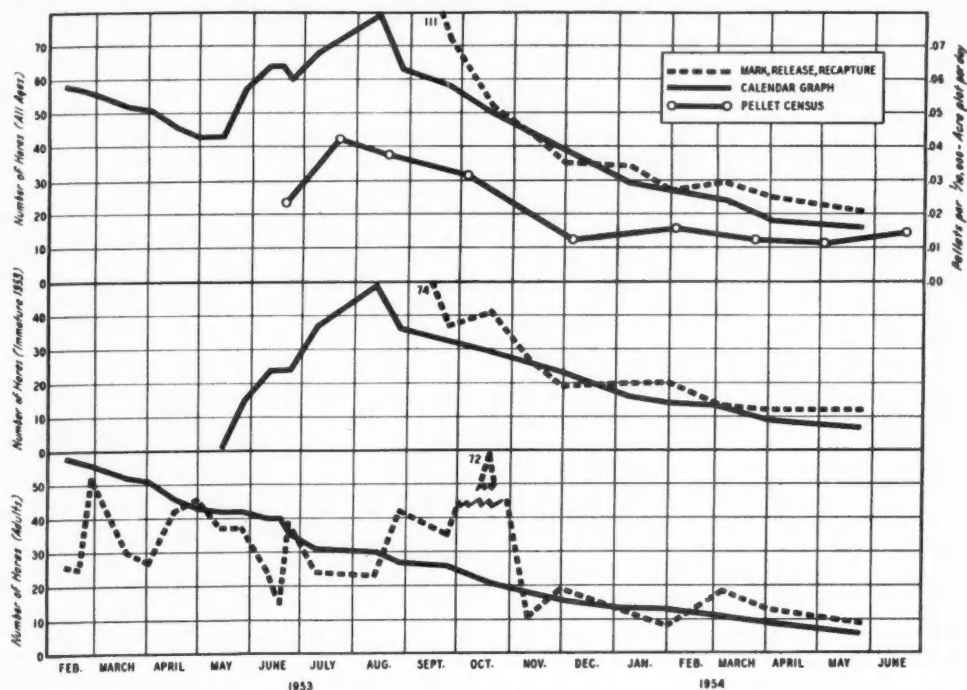


FIG. 9. Snowshoe hare numbers during the period of the study as estimated by the recapture and calendar-graph methods. Mean pellet numbers are estimated from pellet counts on the 1/10,000-acre plots. Bull Island, Flathead Lake, Montana.

total hares, 74 for immature hares). It is less apparent in September, and apparently ceased to influence the estimates from October on. Except as noted, the recapture and calendar-graph estimates run remarkably parallel courses after October.

The fecal pellets on Bull Island were sampled nine times from July, 1953 to July, 1954. Three hundred and sixteen sample plots were located systematically (shown by the small dots, Fig. 3). The plots were circular, 1/10,000-acre in size, and marked by an iron spike at the center. The plots were cleared of all old pellets on or about June 3, 1953, so that the pellets subsequently counted were of current production. Thereafter, these new pellets were removed from the plots when they were counted to make way for the following count. The pellet counts were made on the dates shown in Table 7. These counts were averaged over the total plots and over the days elapsed since the previous count. This gives the mean number of pellets per plot per day during the period of pellet production. Fiducial limits (two standard errors) were calculated for the mean number of pellets per plot. These were then divided by the number of days elapsed since the last count to obtain confidence limits for the mean number of pellets per plot per day.

The means of pellets per plot per day are plotted in Fig. 9, upper part. The points selected on the

TABLE 7. Snowshoe hare pellet samples from 316 1/10,000-acre plots on Bull Island, July, 1953 to July, 1954.

Date	Total No. Pellets	Mean No. Pellets/Plot	No. Days Elapsed	Mean No. Pellets/Plot/Day*	Fiducial Limits ($\pm 2 \text{ Sm}$)*
July 7-11.....	268	.848	36	.0236	$\pm .0080$
Aug. 4-8.....	373	1.180	28	.0421	$\pm .0127$
Sept. 1-4.....	334	1.057	28	.0378	$\pm .0108$
Nov. 2-5.....	617	1.953	62	.0315	$\pm .0081$
Jan. 5-9.....	253	.801	64	.0125	$\pm .0053$
Mar. 3-5.....	285	.902	57	.0158	$\pm .0084$
Apr. 12-15.....	163	.516	41	.0126	$\pm .0059$
May 23-26.....	147	.465	41	.0114	$\pm .0057$
July 13-18.....	233	.737	51	.0145	$\pm .0056$

* These values can be converted to mean number of pellets per acre per day by multiplying by 10,000.

calendar (abscissa) for this curve are the midpoints between mean sampling dates.

The pellet census method can now be related to the recapture and calendar-graph methods. In general the three methods show similar trends on the graph (Fig. 9, upper). In the period February-June, 1954, the curve of the pellet method approaches those of the other methods more closely than in the earlier periods. This may be accounted for by the fact that the calendar-graph method has a special downward bias as the terminal trapping period is

approached. Also, the pellet method is probably responding to the 1954 recruitment of young hares in its June upswing, while neither of the other two methods has yet responded to that influence. Another possible influence here is that hares with a woodier diet in winter may produce more pellets per hare than they do in summer when they are on more succulent diets. Thus, even where there is less agreement among the methods, the similarity of trend suggests that they are closely related to each other and reflect the behavior of the actual population.

The number of hares can be calibrated in terms of pellet numbers from data shown in the graph. This calibration can then be used in other pellet-sampling projects as a conversion factor to convert pellet numbers into hare numbers. The conversion factor is computed in the following manner. First, both the hare and pellet data are expressed in terms of numbers per acre. Second, each of the pellet numbers is divided by a corresponding hare number and the resulting quotients are averaged to give an average conversion factor. The data and computations are shown in Table 8.

TABLE 8. Computation of conversion factors for converting pellet estimates to estimates of snowshoe hare populations.

Date of Pellet Estimate	Pellets Per Acre Per Day	CALENDAR-GRAPH		RECAPTURE	
		Hares Per Acre*	Conversion Factor	Hares Per Acre*	Conversion Factor
June 21, 1953.....	236	0.62	381
July 22, 1953.....	421	0.72	585
August 20, 1953.....	378	0.72	525
October 5, 1953.....	315	0.55	573
December 6, 1953.....	125	0.38	329	0.35	357
February 4, 1954.....	158	0.27	585	0.27	585
March 24, 1954.....	126	0.20	630	0.26	485
May 3, 1954.....	114	0.17	671	0.23	496
June 20, 1954.....	145
Mean (1st 4 dates)...			516	
Mean (2nd 4 dates)...			554		481
Mean (all dates)....			535	

* Values in these columns are taken from the calendar-graph and recapture curves opposite the dates of the pellet estimates.

It is of interest to compare conversion factors for different periods and for the different census methods. The mean conversion factor for the calendar-graph method is 554 pellets per hare per day. For the recapture method (which has data available only during the December 6-June 20 period) it is 481 pellets per hare per day. Since the calendar-graph method underestimates populations, its conversion factor is expected to be too high; that is, there are too many pellets per hare. This is reflected in the conversion factor of 516 for the earlier period of the calendar-graph, when the bias is less, compared with 554 for the latter period, when the bias is greater.

It would be instructive to compare these conver-

sion factors with actual mean numbers of pellets produced by hares in a day. No information on this point is available from field studies, but daily pellet counts were obtained from penned hares. These were fed commercial rabbit food, apples and canned milk in addition to three species of natural food—creeping hollygrape, yellow pine and Douglas fir. Under these conditions of captivity and food, which was probably less bulky than that obtained in nature, the two penned hares produced respectively an average of 216 ± 53.6 and 233 ± 38.6 pellets per day over a six-day period. Probably pellet production in the field is at a rate somewhere between the mean of 225 per day found in these penned studies and the 480 found in the field studies.

ENVIRONMENTAL FACTORS AFFECTING DISTRIBUTION AND ABUNDANCE

VEGETATION COVER

Casual observations of pellet distribution showed early in the study that they occurred in greatest concentration where trees and shrubs were thickest. Conversely, where trees were sparsely distributed and ground cover consisted of low herbs, pellets were scarce or absent.

This close association of hares and cover is shown quantitatively in Table 9. At each pellet plot, cover conditions were evaluated subjectively as "light," "medium light," "medium," "medium heavy" or "heavy." The term "light" refers to conditions typified by the ponderosa pine habitat—an open stand of timber with only low herbs as an understory and no shrubs. "Heavy" refers to a dense stand of early pole-size Douglas fir reproduction in which the tree crowns are so thickly matted together that little sunlight filters through. Ground cover under this "heavy" canopy is usually sparse because of lack of sunlight, but there is much ground litter of dead saplings and tree limbs resulting from the severe competition among the trees. Intermediate cover conditions, "medium light," etc., are evaluated in comparison with these two extremes of "light" and "heavy." In Table 9 the abundance of hare fecal pellets is shown for each class of cover.

There is a highly significant difference between the mean numbers of pellets under the various cover densities ($F = 8.56$). The difference between the individual pairs of means is significant in only one instance—"medium" vs. "medium heavy" (Table 9)—although differences between means are nearly significant at the .05 level in the lighter densities. There is no significant difference between the "medium heavy" and "heavy" densities.

Pellet abundance increases with cover density up through the "medium heavy" class. In the "heavy" class the pellets tend to be less abundant than in the "medium heavy" class, but are still more abundant than in the three lightest classes. ($P < .05$ for the difference between the means of the "medium" and "heavy" classes.)

Apparently the hares' preference for dense cover has an optimum density stage beyond which increas-

TABLE 9. Average number of snowshoe hare pellets per plot under varying conditions of cover density.

	COVER DENSITY				
	Light	Medium Light	Medium	Medium Heavy	Heavy
Number of Plots.....	38	68	80	59	69
Number of Pellets.....	44	218	401	595	605
Ave. Pellets/Plot.....	1.16	3.21	5.01	10.08	8.77
t (between densities).....	1.81	1.52	2.54*	0.60	

*P = .02

ing density may not improve the habitat. It seems quite likely that the tendency toward diminished use of the "heavy" cover may be attributable to the dense shade which hampers growth of food species at the ground level.

An obvious management practice revealed by these findings is to exercise very light thinning where young pole-size reproduction forms a dense canopy that cuts out sunlight to such an extent that ground vegetation does not grow. Emphasis should be placed on light thinning to leave the cover in the "medium heavy" stage and avoid reducing it to the "medium" or lighter condition. Sixty-nine of the pellet plots on Bull Island were marked by "heavy" cover. This is about 22% of the plots. Presumably about that percentage of the island's 100 acres may be susceptible to thinning treatment to favor hares.

Further opportunities for habitat improvement are apparent in the areas of "light" cover. Typically this cover occurs on the southwest slopes in the ponderosa pine type. Scattered about this slope are small isolated clumps of dense Douglas fir reproduction which furnish good hare cover as evidenced by the pellets on the ground under these clumps. The establishment of more such loci of dense cover would allow an increase in hare numbers on the southwest slope.

PHYSICAL OBSTRUCTIONS

In general field observations it appeared that hare distribution was strongly influenced by physical obstructions. Obviously a hare cannot occupy the space already occupied by a tree trunk or a boulder. Less obviously a hare does not use a space occupied by a collection of small stems into which it would have to push its way against the stems. For example, the interiors of thickets of snowberry, even in areas heavily populated by hares, often showed little signs of hare occupancy.

On each 1/10,000-acre plot (except those in the yellow pine type) the percentage of the area barred to hares by physical obstructions was estimated. Estimates were made by 10% classes in the field and summarized by 20% classes (Table 10). Field observations suggested that the number of pellets would be inversely proportional to the percentage of physical obstruction. This expected relationship was not borne

out. The means in Table 10 are not significantly different from each other ($F = 1.09$).

TABLE 10. Average number of snowshoe hare pellets per plot under varying conditions of physical obstruction.

	PER CENT OF PLOT BARRED BY PHYSICAL OBSTRUCTION				
	0-19	20-39	40-59	60-79	80+
Number of Plots...	144	43	39	20	15
Number of Pellets...	984	362	239	126	32
Ave. Pellets/Plot...	6.8	8.4	6.0	6.3	2.1

Two explanations may exist for this lack of agreement between casual observations and the facts revealed by measurements. First, the obstructions must apparently be extremely dense to bar hares, and the situations where such densities occur are rare. Only 15 plots fell in the 80+ percentile class. Only two of these were occupied 100% by obstructions. Probably a larger sample of this densely obstructed stratum would show it to be used significantly less than the other strata. Second, the thickets with densities less than 80% usually had networks of faint hare trails through them which did not appear upon casual observations, but which were used enough to accumulate considerable numbers of pellets.

In view of the great density of obstructions required to bar the hares and the small part of the area occupied by such densities, it is concluded that physical obstructions do not have appreciable influence on hare abundance and distribution. Indeed, in view of the requirements for dense cover reported in the previous section, the existence of the trunks and stems supporting vegetative cover may be an asset.

THE FOOD-COVER-PREDATOR COMPLEX

In general the abundance of hare food varies inversely with the density of cover. Many food plants do not thrive under dense cover; those which do grow there are utilized so intensively that most of their accessible parts have long since been exhausted. Therefore the hares are often attracted away from cover to get at the food plants which grow more abundantly and accessibly in the open. For example, in summer the petioles of balsamroot are relished by the hares; balsamroot is strikingly intolerant of shade and grows best in treeless, shrubless areas. Again, at a certain time in fall the hares brave otherwise unfrequented openings to eat junegrass (*Koeleria cristata*).

When a hare moves out into open habitats, its vulnerability to predators can be expected to increase. Thus the hare population at any given instant is subject to a complex co-action involving food, cover, and predator-prey interactions. Hare distribution is the result of delicate adjustments among the spatial relationships of these various control factors.

POPULATION FORCES

The size of a population of animals is considered to be the resultant of three forces—reproduction,

mortality, and movements. These forces are in turn influenced by the environmental factors, habitat, predation and competition. In the following sections some of these forces and factors are described for the snowshoe hares of Bull Island. Conditions in the Bull Island population are compared with those in other localities whenever comparative data are available from related studies.

REPRODUCTION

Breeding Season. The onset of the breeding season is indicated in the male by the enlargement of the testes and their descent into the scrotum. Later the females show their first evidence of pregnancy—palpable embryos and enlarging mammae.

In 1953 in Montana the first enlarged testes were observed on February 18. From that date until the end of the next trapping period (February 25-27) the males displayed varying stages of testes enlargement and descent. Some were fully enlarged and descended, others were in intermediate conditions. When trapping was resumed on March 17, all males that were caught had fully enlarged and descended testes. In 1954 testes were in inactive condition at the close of the trapping period which extended from January 29 to February 1. At the start of the next trapping period, March 3, nearly all testes were fully enlarged and in scrotal position. A few were not fully active. None was in inactive condition.

These observations indicate that the males become sexually active in the latter half of February and early March. Criddle (1938) reports that males become sexually active by mid-March, earlier or later depending on the mildness of the spring weather. Aldous (1937) describes the chronology for Minnesota where the testes descended in late February and reached full size in March. Severaid (1942) found that the mating season started in Maine "about the first of March."

Uterine conditions of pregnancy become palpable some time after pregnancy begins. Just how long this period may be is not known. Green & Evans (1940b) estimated that visible pregnancy in dissected females begins about five or six days after the actual beginning of pregnancy. Pregnancy apparently becomes palpable at about the same time that it becomes visible on dissection, so that six days may be taken as the period of lag between the onset of pregnancy and its initial palpability.

The first palpable pregnancy in 1953 in Montana was recorded on March 19. During the trapping period March 17-20, 10 females were caught and palpated for embryos 15 times. Three of the 10 females were recorded as pregnant, although two of these pregnancies were considered questionable. The third pregnancy was considered to be more certainly present as it was accompanied by enlarging mammae. All pregnancies were in early stages as indicated by the small size of the embryos, the condition which made the tactual findings uncertain. On the basis of the above chronology of first pregnancies and the time-lag assumption, it appears that pregnancies began in

1953 approximately six days prior to March 19, or about March 13.

In 1954 no traps were set in mid-March to test for earliest pregnancies. Traps were set March 31 to April 3. Six females were caught and palpated: four were pregnant, two were not. It appears from this that the time of first pregnancy varies among the females over a period of perhaps three or four weeks. Apparently the females do not start to become pregnant until almost two weeks after the males display evidence of sexual activity. Criddle (1938) reports first matings start in southern Manitoba in late March and early April on the average. MacLulich (1937) states that there is no pregnancy before late April in northern Canada and suggests that northern hares start to breed later than southern ones. Green & Evans (1940b) found no pregnancies earlier than March 27, and Aldous (1937) gives March 24 as the earliest known pregnancy then available for Minnesota and Wisconsin. Severaid reports coitus at an earlier date (February 25 and March 2) in Maine, but in both instances pregnancy did not result. His earliest record of pregnancy was March 20. In a later paper Severaid (1945) reports a birth as early as April 17, which would place impregnation at about March 12 at the earliest. Apparently the breeding season started at about the same time in all these studies except those of MacLulich.

The breeding season terminates in July. The last record of enlarged, scrotal testes was on July 10 in 1953 and on July 15 in 1954. In both years the frequency of trapping was light at this time and fewer adult than immature males were captured, so that the date of testes regression cannot be fixed with great precision.

The latest records of pregnancy were July 10, 1953, and July 13, 1954. Of eight adult female hares examined August 12-14, none was pregnant (but all were lactating). Again the interference of immature hares and the light trapping frequency prevent precise analysis of the date of termination of pregnancy. Apparently it terminated about August 1, which indicates cessation of breeding activities in late June or early July. Since enlarged, scrotal testes occurred in males as late as July 16, it appears that the period of mating activity may last longer in males than in females.

In southern Manitoba Criddle (1938) recorded pregnant females as late as September 23 and he stated that pregnancy may continue even into October. MacLulich (1937) also reported a few births occurring in August and September. Green & Evans (1940b) found only a negligible number of pregnancies after July 31 among 230 females examined in seven years. However, this estimate was based on females caught in the wild and included non-breeding young of the year. Among their captive adult females 10-20% gave birth during August. Aldous (1937) reports a pregnancy near term as late as August 31 in Minnesota. This was an exceptional case, however, and most of his late-pregnancy records occurred in early August. Grange (1932) had a captive female that

gave birth on August 18. Severaid (1942) reports that the hares produce young until August in Maine. These findings suggest that as the onset of breeding is earlier in Montana than at other stations, so the termination of the reproductive period is also earlier than it is at the other stations.

The occurrence of lactation was observed during the 1953 reproductive season. Females were regularly tested for lactation by "milking" the mammae. Usually milk could be extruded if the animal was lactating. Occasionally a female would fail to yield milk even though the condition of the teats showed evidence of recent suckling (hair matted about teats as a result of wetting during suckling and subsequent drying). In these cases the animal was considered to be lactating even though milk could not be produced.

Lactation was first observed during the trapping period April 28 to May 1. Of seven females examined then, two were lactating, five were not. Thereafter and until September 22 practically all adult females examined were lactating. During that period (May 11 to September 22) 21 adult females were examined 98 times. Only three times was a female recorded as "not lactating." It should be emphasized that in these three instances the animals may have been lactating even though the teats did not indicate it. On the other hand it is possible that if a female loses her young or weans them any considerable time before the subsequent litter is born, she may cease lactating temporarily. The last lactation was observed on September 22.

Severaid (1942) reported that in captivity pregnant females weaned their young at the 25th to 28th day of nursing. He does not say whether lactation continues after weaning. The low prevalence of non-lactating females suggests that lactation did continue in the Bull Island hares. Had lactation ceased with the termination of nursing, there would have been a period of non-lactation of about 11 days out of 37, nearly 30% of the time. Since only 3% of the tests for lactation gave negative results, it is concluded that the hares usually lactate continuously during the breeding season.

It appears that the young of the last-born litter nurse longer than those of earlier litters. There are four records from Bull Island sufficiently detailed to indicate terminal nursing periods of not less than 41, 46, 46 and 47 days respectively. Severaid (1942) reported that non-pregnant females allowed their young to nurse as long as 41, 42 and 56 days in certain cases. Grange (1932) reported a terminal litter which was nursed "for more than six weeks, and probably . . . up to fully two months of age."

Apparently the females of the Bull Island population were in continuous process of pregnancy and lactation from March to October, i.e. seven months.

Number and Size of Litters. The average number of litters born per female in 1953 was estimated by the method of Green & Evans (1940b) in which

$$I = \frac{\sum (PD)}{G}$$

where I is the average incidence of pregnancy, P is the prevalence of pregnancy at a given period, D is the number of days in the period, and G is the length of the palpable gestation period which is here taken to be 30 days. In the present study the period included one trapping period plus one-half the days since the last trapping period and one-half of the days until the next trapping period (Table 11). Dividing 88.32 by 30, the incidence of pregnancy is found to be 2.9 pregnancies per female for the breeding season of 1953.

TABLE 11. Computation of the incidence of snowshoe hare pregnancies on Bull Island in 1953.

Dates	Number of Days (D)	Number of Females Examined	Number Pregnant	Prevalence of Pregnancy (P)	PD
April 8-April 22.....	15	5	5	1.00	15.00
April 23-May 6.....	14	7	6	.86	12.04
May 7-May 20.....	14	6	6	1.00	14.00
May 21-June 3.....	14	9	9	1.00	14.00
June 4-June 14.....	9	10	6	.60	5.40
June 15-June 21.....	5	10	7	.70	3.50
June 22-June 30.....	9	7	6	.86	7.74
July 1-July 26.....	26	11	7	.64	16.64
Total ($\sum (PD)$)...					88.32

Criddle (1938) estimated the number of litters as at least 3, often 4 and occasionally 5. MacLulich (1937) indicated that the Ontario hares had about 3 litters per year. Aldous (1937) thought that "In the absence of actual data the normal yearly number of litters for each female would appear to be between two and three. Probably two litters would be more nearly the rule than three." Green & Evans found an incidence of 2.3 for the composite of their seven-year study. Severaid (1945) records 3.0 litters per female in 17 captive females in 1940; in 1941, 16 females had an average off 2.75 litters.

Data on the number of young per litter were obtained by counting embryos by palpation. No opportunity was afforded to test this method against actual dissections, so the extent of inaccuracy is unknown. Some evidence of the precision of the method is provided by repeated counts during a single pregnancy. In 16 individual pregnancies, palpation counts were made on two or more different dates. The counts are shown in Table 12. The variability of these observations is large and indicates low reliability of individual counts. However, the mean counts do not vary significantly ($F = 1.63$, d.f. = 4, 42). Practice in palpating embryos prior to visual counts after dissection may serve to refine the technique and to determine its reliability.

The average number of young per litter as palpated in 32 pregnancies in 1953 was 2.72 (Table 13). In 1954, 9 pregnancies had an average palpation 3.00 embryos. Other investigators have reported mean litter sizes from 2.88 to 4.00 embryos (Table 14). While no tests of significance are possible because insufficient information is published, it appears

TABLE 12. Counts of snowshoe hare embryos made by palpation at different times on 16 different pregnancies, showing the variability of results by the palpation method.

Pregnancy No.	PALPATION TEST NUMBER				
	1st	2nd	3rd	4th	5th
1.....	1	2	2		
2.....	2	1			
3.....	2	2-3	3		
4.....	3	5	4	3-4	
5.....	2	3	4		
6.....	3-4	1-2			
7.....	4	3+			
8.....	1	0	3	3	3-4
9.....	2	2			
10.....	1	1	1	3	3
11.....	4	3			
12.....	4	4			
13.....	2	3	3	4	
14.....	1?	3			
15.....	3	2	3		
16.....	3	3	3		
Ave.....	2.41	2.44	2.89	3.40	3.25

TABLE 13. Frequencies of occurrence of snowshoe hare embryo counts per pregnancy in 1953, 1954 and the total for both years.

No. of Embryos	FREQUENCY		
	1953	1954	Total
1.....	4	2	6
2.....	7	1	8
3.....	15	2	17
4.....	6	3	9
5.....	0	1	1
Total.....	32	9	41
Mean.....	2.72	3.00	2.78
95% Conf. Lim.....	.32	.92	.31

that some of these mean litter sizes may be significantly different from others. The variations show no apparent geographic or chronological trends.

Nests. Places of birth of snowshoe hares have been variously described. Some of the earlier reports indicate that a nest is constructed in litter and ground cover with fur lining provided by the mother. But all the more recent investigators (Seton 1953, Grange 1932, Aldous 1937, Severaid 1942) agree that no nest is made. I found no nests during the present study. The youngest hares found in the wild state were usually old enough to be moving about and were found in casual circumstances that gave no hint of a nest. In 1951 a small clearing was being made for a cabin at Holland Lake several miles east of the site of the present study. A small pile of evergreen saplings was left in the clearing one week-end. One week later when the brush pile was moved, four small hares, considered to be about four days old, were dislodged. No nesting material was found, but apparently the brush pile had been used as a "nursery."

TABLE 14. Mean snowshoe hare litter sizes reported by other investigators.

Authors	Mean Number Embryos Per Pregnancy	Number of Pregnancies Tallied
MacLulich (1937) Manitoba.....	4.00	27
Criddle (1938) Manitoba.....	3.35	153
Aldous (1937) Minnesota.....	3.29	?
Grange (1932) Wisconsin.....	3.00	6
Severaid (1942) Maine.....	2.92	161
Green & Evans (1940b) Minnesota.....	2.90	140
MacLulich (1937) Ontario.....	2.88	25

Development. A comparison of weights of young hares at birth is presented in Table 15. Those of the Montana hares are strikingly smaller than the others. This small birth weight in Montana stock is corroborated by the weights of other hares which were weighed within a few days after birth. A hare captured near Deer Lodge, Montana, gave birth to four young at the Northern Rocky Mountain Laboratory of the U. S. Public Health Service on June 28, 1952. Four days later two of these weighed 46.0 and 62.6 gm respectively, an average of 54.3 gm. The hares captured at Holland Lake which were thought to be about four days old weighed 67, 57, 54, and 60 gm respectively, an average of 59.5 gm.

TABLE 15. Weights (in grams) of snowshoe hares at birth.

Investigators	Location	Individual Weight (Grams)	Ave. Wt.
MacLulich (1937).....	Ontario	49, 48, 58	51.7
Grange (1932).....	Wisconsin	85.0	85.0
Grange (1932).....	Wisconsin	75.3, 75.4, 80.4	77.0
Severaid (1942).....	Maine	(128 hares)	67.0
Adams.....	Montana	40.6, 40.4, 37.7	39.6

Each time a hare was trapped on Bull Island its weight was recorded. From these data an attempt was made to plot a growth curve. Since in no case was the date of birth known, recourse was had to an approximation of the growth curve, using the form of Severaid's (1942) curve in the following manner. It was assumed that the Montana hares grew at approximately the same rate at any given age as did Severaid's hares in Maine. A curve was therefore constructed analogous to Severaid's curve, but with the origin lowered to the level of the birth weights for Montana and with the right hand end of the curve lowered to the average weight of the Montana juvenile hares in late winter (Fig. 8).

The goodness of fit of this modified curve for Montana hares was tested in the following empirical way. The weight of each hare at its initial capture was placed on the curve at the appropriate weight ordinate, letting the point fall on whatever date ab-

seissa it would. This in effect assumed that all hares fell on the weight-age line at the time of initial capture. At subsequent captures their weights were plotted according to the number of days since the last weighing and at the correct weight ordinate, regardless of where the point might be with regard to the growth curve. It was postulated that, if a hare was growing more slowly than the rate indicated by the modified Severaid curve, the points subsequent to the one plotted from the initial weighing would fall below the line. And conversely, if a hare grew at a more rapid rate than the line indicated, the secondary points would fall above the line. If the rates of growth of Montana hares coincided with the rate indicated by the line, there would be approximately as many points above the line as below it. Inspection of the curve shows that the goodness of fit varies at different sectors. From birth to about the 50th day, nearly all points fall below the curve. Apparently the curve is too steep in this sector, which may indicate that the Montana hares develop more slowly than those in Maine during their early growth. From 50 to 100 days the line appears to fit the data fairly well. After the 100th day the points become widely scattered so that it is difficult to evaluate the curve. This situation is apparently comparable to that observed by Severaid (1942) who reports, "Whereas most healthy hares showed a consistent gain during the first 12 to 14 weeks, their weight was irregular in the weeks following." Weights of some of the hares fluctuate violently at this time, the average effect of which is a slight dip in the curve. This dip was not allowed for in drawing the present curve, but its presence is indicated by the collection of low points between the 100th and 160th days.

Findings of the Montana study indicate that growth ceases on the average at about 1,000-1,100 gm. Those hares born early in the summer reach maximum weight in fall and early winter. Hares born later continue to grow through most of the winter. This sequence of growth among individuals was illustrated by an analysis of 23 hares born in 1953. These hares were listed in order according to their average weights during the period September 22-November 11, 1954, the heaviest hare at the top of the list and the lightest at the bottom. The hares were then divided into two groups—the 11 heaviest individuals in one group, the 12 lightest in another group—and the weight of each individual was compared with its weights later in the winter. It is assumed that the animals in the "heavy" group were older and that those in the "light" group were younger; this is supported by their birth dates as estimated from the growth curve at the time of their first capture. The hares in the "heavy" group gained an average of only 5.1 gm during the interval studied, whereas those in the "light" group made an average gain of 56.7 gm. (It is interesting to note that during the same period seven adult hares born prior to 1953 lost an average of 16 gm.)

The greater weights of the Maine hares than those of Montana may be attributed to the fact that the

former were raised in captivity. Severaid (1942) reported that 153 wild adult hares caught in February (1940 and 1941) had an average weight of 1,229 gm, while 38 captive hares weighed in February and December (1940) had an average of 1,636 gm. In Montana, the 36 hares live-trapped in January and February (1953-54) had an average weight of 1,132 gm (S. E. = 20.48). The upper confidence limit (95%) of the mean (1,171 gm) is so close to the lower confidence limit of Severaid's mean for wild hares that it is doubtful that a significant difference could be demonstrated. Furthermore, Severaid presents data on the length of hind feet and of ears that are quite comparable with those for Montana hares. The mean length of ear (from notch) for 29 adult hares in Maine was 73.0 mm. In Montana it was 72.9 mm. The mean length of the hind foot was 137.0 mm in Maine, 136.7 in Montana. These measurements show greater similarity between the two groups of hares than did the weights and substantiate the idea that the Maine and Montana hares are about the same size on the average.

Green, Larson, Bell & Evans (1938) and Green, Larson & Bell (1939) report the mean weight of 153 healthy, non-pregnant wild hares from Minnesota as 1,402 gm (range: 1,000-1,900 gm). Grange (1932) states that "The average northern Wisconsin hare will probably run from 1,400 to 1,600 gm." These weights appear to be distinctly greater than the mean weight of either the Montana or the Maine wild-caught individuals.

Sex. Snowshoe hares can be identified as to sex at all ages and all times of the year only by anatomical characteristics of the everted penis and clitoris. Identifying characteristics have been described and illustrated by Severaid (1942). Sexes can also be distinguished in adults in the breeding season by the presence of scrotal testes in males and enlarged mammae in females.

The sex ratio of the 58 hares known to be alive at the start of the project in February, 1953, was 29 females to 29 males. However, the month-to-month trapping records showed strongly unbalanced sex ratios (Table 16). Apparently the males are more readily trapped in the spring than are the females. Later, as summer approaches, the females become more susceptible to trapping than the males. From February to April there were more males caught than females. From May to August the reverse was true. This demonstrates a marked difference in seasonal effect on the two sexes in their response to trapping. Probably this can be attributed to influences of the mating season. The males begin to travel away from their home ranges when their gonads become active. Perhaps these increased movements bring them into contact with more traps. Later, as the females start bearing young they may require more food and be attracted to the traps more strongly by the bait.

The sex ratio of the 101 young trapped in 1953 was 43 females to 58 males. This is not significantly different from an even ratio. There were no seasonal aberrations in the trapping returns of the sexes in

TABLE 16. Sex ratios of adult snowshoe hares of 1953 as indicated by monthly trapping records in comparison with the "known" ratios shown by the calendar graphs.

Month	TOTAL MONTHLY CATCH		SEX RATIO ACCORDING TO CALENDAR GRAPH		P
	Males	Females	Males	Females	
February.....	10	7	29	29	.3 > P > .2
March.....	17	6	27	29	.1 > P > .05
April.....	14	11	24	27	.7 > P > .5
May.....	10	13	22	21	.95 > P > .9
June.....	7	13	21	21	.5 > P > .3
July.....	3	12	18	15	.1 > P > .05
August.....	8	12	18	13	.5 > P > .3

P—Probability that the monthly-ratio sample is drawn from the same population as the calendar-graph ratio (chi-square test).

the young hares comparable to those that appeared in the adults.

Webb (1937) used the data of Green and Aldous to show that in Minnesota a similar seasonal sexual variation occurred in response to traps over a 5-yr period and suggested essentially the same explanations for it that I have just outlined.

Age. In the present study two criteria were used to distinguish young of the year from older animals: (1) the color of the hind feet, and (2) the condition of the teats in females.

Nelson (1909) pointed out that in northern and high mountain forms of snowshoe hares the feet of adults are white while the feet of young hares before their first fall molt are brown. This distinction was fairly reliable in the Montana hares studied. During the summer of 1953 hind foot color was recorded for 69 immature hares and 23 adults. All of the adults had some white on their hind feet. Sixty-four (93%) of the immature hares had no white on their hind feet. Thus it would appear that if a population were classified on the basis of the hind foot color alone, about 7% of the immature hares would be classed as adults and none of the adult hares would be classed as immature. It may be worth noting that those immature hares that had some white on their hind feet had relatively little of it. Similarly, some adults had partly brown hind feet, but always there was more white than brown. It appears, therefore, that a more refined measurement of the amount of white on the feet would give a better discrimination of ages.

During the winter of 1953-54 it became apparent that the ages of females might be distinguishable by the fact that the adults, which had borne young the previous summer, had slightly enlarged teats which were palpable beneath the fur while the immature hares' teats were not palpable. Sixteen female hares known to have been born the previous summer and nine known adult females were tested for palpability of their teats. Only one (6%) of the 16 immature hares had palpable teats. Conversely, all but one (11%) of the adults had palpable teats. This indicates that it would probably be feasible to classify female hares as adult (having bred) or immature (not having bred) by the palpability of their teats.

Further tests of this method are needed. The two misclassifications may have been results of errors in recording, so that the technique may be even more reliable than is here indicated.

In the Bull Island population the ratio of adults to the young of 1953 varied greatly from June 1, 1953 to May 1, 1954 (Table 17). Until the breeding season and the birth of new hares, the population was, of course, all adult. By June 1 there were about 17 young to 41 adults (calendar-graph, Fig. 9). The ratio of young to adults increased thereafter until August when it was 45 young to 30 adults. From September to December there were about $\frac{1}{3}$ more young than adults. Then the ratio dropped to only slightly more young than adults, a condition which persisted into the 1954 breeding season.

TABLE 17. Age ratios of living young and adult snowshoe hares on Bull Island, Montana, by monthly intervals, June 1, 1953 to February 1, 1954.

Date	Hares	Per Cent Young in Population
June 1, 1953.....	59	29.3
July 1, 1953.....	64	46.9
August 1, 1953.....	75	60.0
September 1, 1953.....	62	56.5
October 1, 1953.....	56	55.4
November 1, 1953.....	46	58.7
December 1, 1953.....	39	59.0
January 1, 1954.....	31	54.8
February 1, 1954.....	28	50.0

BEHAVIOR

Home Range. The following analysis of home range from live-trapping data has two objectives, (1) to determine the size of the home range, and (2) to determine whether there are differences in ranges among age- and sex-groups.

There have been many recent evaluations of methods of analyzing home range. Stickel (1954) has reviewed these evaluations and added some of her own. It is generally conceded that at best some of the methods of analysis are of unknown accuracy and at worst many are grossly misleading. For the analysis of home-range size I have used the exclusive boundary strip method.

At times hares travel exceptionally long distances between captures, usually without a return trip to the original home range. These movements are considered to be dispersals and are not included in the computation of home ranges by the exclusive boundary strip method.

Stickel (1954) has emphasized the fact that estimates of home range size increase with the number of recaptures, rapidly at first, then level off to an asymptotic value which approximates more or less closely the true home range. By plotting apparent range size over number of captures it is possible to determine whether the asymptote has been reached and hence

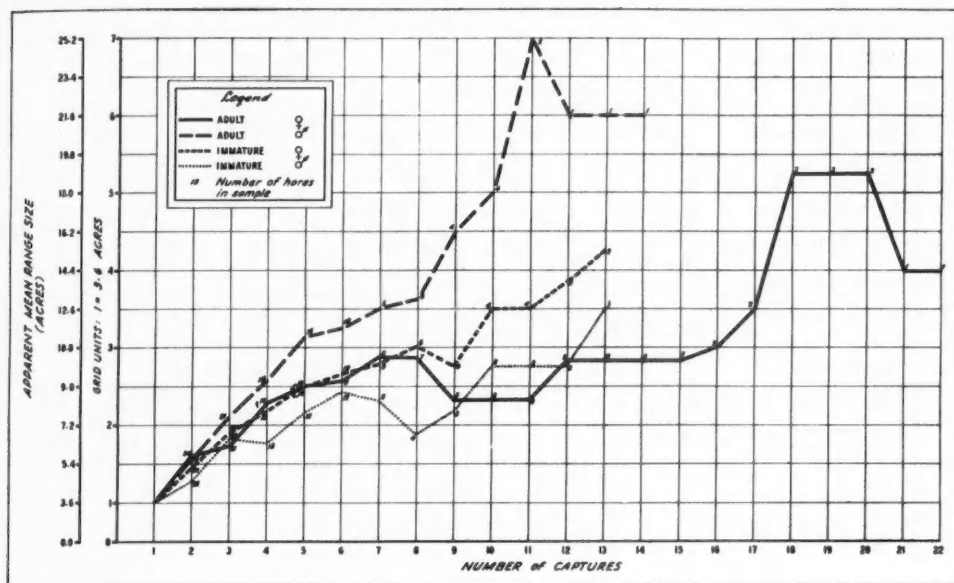


FIG. 10. Apparent size of home ranges of adults and immature snowshoe hares of either sex as indicated by cumulative captures. Bull Island, Flathead Lake, Montana.

whether the full range size is approximated with the data at hand.

In Fig. 10 the data for four groups of hares are plotted as described. Adults and immature hares are plotted separately and within each of these groups the males and females are also plotted separately. It is not clearly apparent in any of the four sex-age groups that the lines have reached the asymptote. The lines for adult males and females show tendencies toward the right side of the graph (indicated by the numbers on the graph) are too few to warrant any conclusions on this point.

The maximum home range values shown in Fig. 10 (adult males, 25.2 acres; adult females, 18.9 acres; immature males, 12.6 acres; immature females, 15.3 acres) are probably smaller than the actual home range sizes. Despite the fact that actual home range size cannot be accurately approximated, certain comparisons can be made among the four groups. For instance, it seems reasonable to assume that a steeply-ascending line is associated with larger range size. This assumption is based on the idea that the hares with larger home ranges would be more likely to be caught at more widely separated trap-sites than would the hares with smaller home ranges. The apparent size of the home range will therefore increase more rapidly with increasing numbers of captures on large ranges than on small ones, thus resulting in steeper curves.

In Fig. 10 the curves for adult females and for immature males and females are of similar steepness. The curve for adult males, in contrast, is decidedly steeper than the others. This implies that the adult males hares have larger home ranges than the others.

Seton (1953) estimates the home range of snowshoe hares to be about 20 or 30 acres in brushy woods and twice that large in more open woods. Criddle (1938) gives the radius of movements within the home range as a few hundred yards in dense woods to a mile or more in thin woods. MacLulich (1937) gives a few random observations of hare movements, which indicate that the hares he studied ranged over areas of only a few hundred yards radius. Aldous (1937) found by re-trapping hares that most (69%) of the recaptures were within $\frac{1}{8}$ mile of the release point. This shows a tendency toward a restricted range size, but no estimates of range area were made. Grange (1932) followed a hare for 1 and $\frac{1}{4}$ hours in falling snow and could not drive it beyond a 10-acre, which he believed gave an indication of the hare's home range.

Another method of comparing home range size is by the analysis of the distance between capture sites (Davis 1953). In this analysis the distances between successive recaptures were averaged for all recaptures of all hares in each age-sex group. No allowance was made here for chances of recapture at various distances as recommended by Davis, because the effect of trap numbers was probably masked by the greater effects of habitat and because the effects of chances of recapture, habitat, and most other variables were operating similarly on all age-sex groups. Davis' method was further modified in that actual distances between the two traps of capture and recapture were used as the basis for grouping capture frequencies.

Frequencies of captures at stated recapture distances are shown in Table 18. Recapture at zero distance occur more frequently than at any other dis-

tance in all age-sex groups except in the adult males. The mean distance between recaptures for adult males (353 ft) is highly significantly greater ($P < .001$) than for adult females (229 ft), immature males (200 ft), or immature females (198 ft). The latter three groups are not significantly different from each other ($F = 0.39$). These findings agree with those of the exclusive boundary strip method.

TABLE 18. Frequencies of recapture of snowshoe hares at various distances according to sex and age.

Distance Between Traps (feet)	NUMBER OF RECAPTURES			
	Adults		Immature	
	♂	♀	♂	♀
0	50	79	71	53
396	64	49	23	24
560	20	7	7	10
792	6	7		2
885	9	1	1	
1088		1		1
1188	1	1	1	
1252				
1428		1	1	
1584	1			
1633				
1680	1			
1771			1	
1980				
2019				
2133				
2240				
2309				
2376				
2409				
2505				
2536				
2656				
2772				
2800			1	
2856+				
Mean	353	229	200	198

There is much overlapping of the ranges of individual hares. This is made evident in two ways, (1) by the size of range in relation to total area of habitat available, and (2) by the capture of several different hares at each trap site.

The total area of hare habitat on Bull Island is 81 acres. (This is the total area of the island, 98.8 acres, minus the area of the relatively uninhabited ponderosa pine type, 17.8 acres.) If home ranges are assumed not to overlap, the values of the ranges shown in Fig. 10, when divided into total habitat acreage, provide a population estimate of 3.2 adult males, whereas the calendar-graph technique gave estimates of as many as 40 adult males in February, 1953, and of not less than 11 in December, 1953. Similar comparisons can be made for each of the other sex-age groups and for the population as a whole. In each case, the estimated number of hares on the island exceeds the available number of exclusive home ranges. Home ranges evidently overlap.

Further evidence of overlapping home ranges is provided by the fact that different adult hares are frequently caught at the same trap-site (Table 19). In the course of typical trapping periods, usually 4 nights, as many as three different individuals have been caught at a single trap site. During the 1953 breeding season there were 91 periods in which only one hare was caught at a trap, 24 periods in which two hares were caught, and 8 periods in which three hares were caught. The same general trend appears also in the other two seasons studied. A test of the interactions between sexes in the multiple captures (Davis 1955) indicated that two males were captured at the same site trap more frequently than expected, two females about as expected, and a male and female less frequently than the calculated expectation. This apparent attraction between males and repulsion between the sexes, which were significantly great (χ^2 probability $< .01$), cannot be readily accounted for biologically. Indeed an opposite trend would have been more logically anticipated. This relationship apparently exists in both the breeding and nonbreeding seasons.

The fact that hares' ranges overlap should not lead to the conclusion that the individuals exert no repulsion toward each other. There is good evidence that the hares resist crowding. Hares are well dispersed over the available habitat, showing no appreciable tendency toward "herd" or "flock" formation. Further evidence is furnished by the behavior of hares brought into close contact with each other. On several occasions two hares have been caught simultaneously in a trap. Invariably when this occurs there is evincing of physical strife. Usually one of the pair is badly lacerated, apparently a result of the kicking and support the hypothesis that conflict results when hares are closely associated. Seldom is more than one hare in view at one time in the field. Occasionally I have seen two at one time, but they were rarely less than several yards from each other. Once I saw three hares together in a small ($\frac{1}{10}$ acre) Douglas fir thicket. They were all within 20 ft of each other. As they flushed, one ran within 3 ft of another; the latter aimed a kick in the general direction of the intruder as they both ran away, possibly an act of repulsion. It appears, then, that snowshoe hares may have a territory (protected part of the home range) which falls into Dice's (1952, p. 247) category number 7—the area around the individual itself.

MacLulich (1937) found no evidence of territoriality. Severaid (1942) does not discuss the subject but pictures two hares resting side by side in a shelter. These may have been litter mates at an early stage of development. Young litter mates kept together in pens in the current study did not fight, but adults which were strangers to each other fought bitterly when put in a cage together. Grange (1932) concluded from observations on captive hares "that there are periods (breeding season for males and during pregnancy for females) when definite hostility to other individuals is shown, but that ordinarily snow-

TABLE 19. Frequencies of single and multiple captures of adult hares at individual trap sites.

Nos. of Hares Caught at Individ. Stns.		FREQUENCIES OF CAPTURES											
		Breeding season 1953 ¹			Non-Breeding Season 1953-54 ²			Breeding Season 1954 ³			All Seasons		
		Total	Ave. ⁴	%	Total	Ave. ⁴	%	Total	Ave. ⁴	%	Total	Ave. ⁴	%
♂	♀												
0	1	53	4.8	43.1	17	4.2	25.0	11	2.8	29.7	81	4.3	35.5
1	0	38	3.5	30.9	16	4.0	23.5	21	5.2	56.8	75	3.9	32.9
2	0	11	1.0	8.9	10	2.5	14.7	1	.2	2.7	22	1.2	9.6
1	1	9	.8	7.3	6	1.5	8.8	2	.5	5.4	17	.9	7.5
0	2	4	.4	3.3	9	2.2	13.2	1	.2	2.7	14	.7	6.1
2	1	3	.3	2.4	7	1.8	10.3	1	.2	2.7	11	.6	4.8
1	2	4	.4	3.3	1	.2	1.5	0	.0	0.0	5	.3	2.2
3	0	1	.1	.8	2	.5	2.9	0	.0	0.0	3	.2	1.3
Total.....		123			68			37			228		

¹ March to October. Seven 4-day trapping periods, four 3-day periods.² November to February. Four 4-day trapping periods.³ March to July. Three 4-day trapping periods, one 5-day period.⁴ Average number of captures per trapping period.

shoe hares are indifferent to one another, or even possibly gregarious."

Movements. Trapping returns show that in addition to movements within the home range hares occasionally move greater distances and establish new home ranges. Seven such dispersal movements were observed. Typically the dispersal maps show a cluster of captures at one or more adjacent traps, then an extended movement to a new locality, followed by another cluster of captures there. Fig. 11 shows this pattern for Hare No. 111. First there is a cluster of captures at traps 7F and 7E. Then the hare dispersed to 6A and was subsequently captured at 6A, 6B and 5B.

There are some minor exceptions to this typical dispersal pattern. Hare No. 227 (Fig. 11) moved from 5D to 2D, followed by what appears to be a shorter dispersal to the area of traps 3C, 2C and 1C. This latter short movement is typical of many movements noted among the entire hare population. Probably these shorter, semi-permanent moves are not actually dispersals. Apparently all hares tend to shift about from time to time, occupying one sector of their home range at one time and another sector at another time. The distinction between this type of movement and actual dispersal may be only a matter of degree.

Another kind of dispersal movement which does not follow the typical pattern was demonstrated by Hare No. 143. Here the captures were all clustered at 1A and 2A except one which occurred at 6A. This hare apparently made a brief excursion outside its range to 6A, then returned at once.

The cause of dispersal movements is not known. They may represent movements of young animals which are crowded out of their ancestral range. Another hypothesis is that they represent movements of sexually mature animals stimulated by a sexual drive at mating time. Of the seven hares observed to disperse in this study, three did so at immature stages of development. The movements occurred at the time of year when the young hares were augmenting the

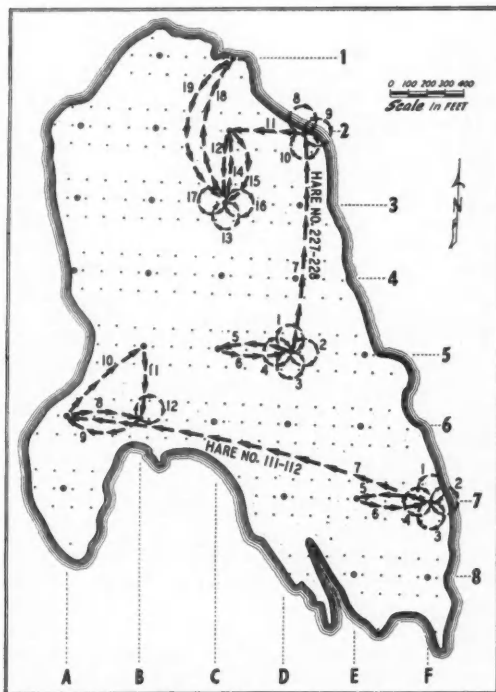


FIG. 11. Dispersal movements of hares 111 and 227. Lines of movement are numbered consecutively in the order of their occurrence between captures. Bull Island, Flathead Lake, Montana.

population in great numbers. The remaining four dispersals occurred in late winter or early spring when the population was at the annual minimum. Presumably no crowding occurred then. However, in these cases sexual activity had just begun, as evidenced by the position of the testes. Although all seven dispersants were males, the chance of randomly selecting that

number from a population of this size, in which the sexes are approximately evenly distributed, is only about 128 to 1. These data suggest that dispersal may indeed be related to sex.

Criddle (1938) reported two periods of migration, mid-February to April and October to December. He believed the former was associated with the onset of breeding, the latter with leaf-fall which stimulated movement to denser cover. Tracks in snow showed where hares had crossed 8-15 mi of open prairie from one wooded tract to another in one night.

Green, Larson & Bell (1939) reported a hare that moved 1 and $\frac{1}{8}$ miles. They considered this an exceptionally long movement. Usually the range of movement between captures was only $\frac{1}{8}$ to $\frac{1}{4}$ mile. Grange (1932) presents reports of trappers that hares cross lakes two miles wide.

Use of Forms. Hares found undisturbed in daytime are frequently resting in their forms. As used here, the term "form" means that spot where a hare rests. A form may have no particular structure, being simply a place where a hare spent a few minutes or hours resting. With repeated use, a slight oval depression may develop in the ground litter or even in the ground where the hare has stood or lain. The only construction effort seen applied to a form occurred once when a twig which had grown up in the desired resting-place had been cut off by the hare.

The extent to which forms were used repeatedly was a subject of inquiry in the present study. When a resting hare was observed, its form was given a number and that spot was checked on subsequent visits and the absence or presence of a hare was noted. This study was started in December, 1952, on the adjacent mainland and continued on Bull Island after February, 1953. During this time 48 forms were observed 710 times. The forms were occupied an average of 15.2% of the times they were observed. About 38% of the forms observed were used only once. Apparently hares often stop to rest at any place they happen to be when a rest period is in order. At the other extreme one hare was observed to use one form on 10 out of 11 successive observations on different days in December, 1952 and January, 1953. Sometimes two or more hares use the same form, though never more than one at a time.

The places used for forms were usually in or near good cover. The frequently-used form mentioned above was beside a boulder about 18 inches high partially screened by a Douglas fir branch. Another form was beside the bole of a juniper tree screened by a log and a low spreading juniper bough. Occasionally hares rested in more exposed situations. One hare was observed on January 21, 1953, perched on top of a boulder about four feet in diameter at the foot of a talus slope. Although there were some shrubs about, they had lost their leaves so that the hare was quite exposed, especially from above.

Resting hares seem very wakeful. I have never seen one asleep with both eyes closed. They seem to doze off for a while, their eyelids drooping and their

eyes acquiring a slightly glazed appearance. Sometimes one eye may close briefly. After a minute or two of this, the hare stirs, fully opens its eyes and looks about. Perhaps a period of hair grooming or reingestion ensues. Then the hare dozes again for a while.

Self Protection. When settling down to rest the hare often rises upon its haunches and tucks its front feet well back under its rump, then lies with its chest and belly on the legs. This position is not unlike that of a hare at the beginning of a leap while running. Thus the resting hare is in a position to start running at an instant's notice.

There are many other safety devices which serve to protect the hare from predators. The selection of proper cover has already been discussed. When approached at a distance, the hare remains immobile, while its protective coloration and the cover help it to elude detection. Approached more closely, the hare resorts to flight. There appears to be an ontogenetic variation in the use of these two devices. Younger animals rely more on hiding; the older ones on flight. This age relationship follows physical development. Infant hares lack coordination and strength to run. As they mature and acquire agility they rely more and more on flight for protection. But protective-concealment reaction always continues to be a major part of the escape pattern. Mr. Lon Fast, a resident near Bull Island, reports that the hares hold to cover sufficiently that his dogs can stalk and catch them in their forms.

Audubon & Bachman (*vide* Grange, 1932) say that, "We are not aware that the [snowshoe hare] ever takes shelter either in a hole in the earth, or in a hollow tree. We have seen it chased by hounds for whole days, and have witnessed the repetition of these hunts for several consecutive winters, without ever knowing it to seek concealment or security in such places." Richardson (*vide* MacLulich 1937) says that "the American Hare does not burrow." Later writers (MacLulich 1937, Grange 1932, and others) state that the hares use burrows, although the extent and purposes of such use are not made clear. On three occasions during the current study, hares took refuge in burrows when pursued by dogs or frightened by the author. On Bull Island, hares were frequently seen resting at burrow entrances, but several deliberate attempts to force them to use burrows failed.

It is doubtful that hares ever dig dirt to any extent. The burrows on Bull Island and the mainland were judged to have been made by badgers. None of those used by hares appeared to be of recent origin. Nor was there any evidence that the hares had effected any recent changes in them. Two burrows thought to have been used by hares were excavated. Both were simple, unbranched passages extending only about 5 ft underground. There was no evidence of a nest, rest-chamber, or any other modification attributable to hare use. Captive hares have been seen making digging motions at their cages with their front feet, but these activities result in very little movement of earth. Young hares have been kept

for many weeks in pens of wire netting with the lower edge of the netting simply in contact with the ground surface. The hares made no attempt to dig beneath the netting. About the only effective earth-moving accomplishment I have observed is at dust baths where rain-hardened crusts often show claw-marks where hares have loosened the dirt.

FOOD HABITS

Observations of food eaten were made as opportunities occurred in the course of field work. Hares found eating were observed with field glasses to discern the species of plants eaten, and remnants of partially-eaten plants gave field clues to food habits.

In Table 20 the species of plants eaten are listed by groups based on amounts eaten in the total annual diet. The ranking is done largely by subjective judgment. Some heavily-used species may be absent from the list because they were eaten in a way that left no evidence. The consumption of very young seedlings, for example, may leave no trace if the entire plant is cut off near ground level. Species which were eaten infrequently may also have been overlooked.

TABLE 20. Species of plants observed to have been eaten by snowshoe hares. The degree of use, season of use, and parts used are also shown.

Species	Season of Use ¹	Parts Used
Heavily used		
<i>Pseudotsuga taxifolia</i>	W	Twig-ends, needles, bark
<i>Berberis repens</i>	W	Petioles, leaves
<i>Balsamorhiza</i> sp.	S	Petioles
<i>Erythronium grandiflorum</i>	Sp	Leaves
<i>Arnica</i> sp.	S	Petioles
<i>Spiraea betulifolia</i>	S	Stems
Moderately used		
<i>Pinus ponderosa</i>	W	Needles, twigs
<i>Amelanchier alnifolia</i>	W	Twig-ends
<i>Arctostaphylos Uva-ursi</i>	S	Leaves
Lightly used		
<i>Penstemon</i> sp.	W	Dried plant
<i>Symphoricarpos albus</i>	W	Twigs (?cut only for trail clearing)
<i>Juniperus scopulorum</i>	W	?
<i>Fragaria</i> sp.	Sp	Leaves
<i>Smilacina</i> sp.	Sp	Stalk, leaves
<i>Taraxacum</i> sp.	S	Leaves
<i>Collinsia</i> sp.	S	Entire plant
<i>Claytonia</i> sp.	S	Stalk
<i>Calamagrostis rubescens</i>	S	Blades
<i>Koeleria cristata</i>	F	Blades
<i>Heuchera cylindrica</i> var. <i>glabella</i>	W	Leaves
<i>Holodiscus discolor</i>	F	Leaves, twigs

¹ W—winter; Sp—spring; S—summer; F—fall

The season of use varies in duration. Douglas fir is eaten over a long period extending from fall to spring. Junegrass is the most restricted in its period of use of all the species observed. Beginning with light utilization in August, the use of junegrass increased until November (1953). In November there

was a brief period when the hares concentrated heavily on the use of junegrass, going out into openings, where they seldom ventured otherwise, to seek the grass.

Reingestion (eating feces) was observed four times during the study of the wild animals and at other times in captive hares. In this practice a fecal pellet is taken directly from the animal's anus into its mouth, chewed up, and swallowed. In what condition the material reaches the stomach is not clear at present. Watson & Taylor (1955) report that special unfed feces are reingested by the European hare in New Zealand. These appear as amorphous masses in the stomach. Mr. C. C. Sperry, of the Fish and Wildlife Service's Wildlife Research Laboratory, has written me that he has found intact fecal pellets in the stomachs of snowshoe hares. However, it appears likely that if the chewing actions I noted are effective the reingested material would be well comminuted in the stomachs of the hares studied here.

MacLulich (1937) reports hares eating sand, sometimes in large quantities. Sand has occasionally been found in the fecal pellets of hares on Bull Island.

MORTALITY

Mortality Rates. Mortality rates are described here in terms of probability of survival, which is the number of hares alive at the end of a period divided by the number alive at the beginning of the period. Both crude and age-specific rates are presented. Sex-specific rates are not given since the sex ratio remained fairly uniform indicating no appreciable differential in mortality between sexes.

In the section on Reproduction it was estimated that in 1953 about 2.9 litters of about 2.6 young each were born per adult female. It is estimated further (calendar-graph) that there was an average of 42 adults during the breeding season, one-half of which (21) were females. At the estimated birth rate, 21 females bore an estimated 158 young.

Only 106 of these young hares were ever trapped, and these were first trapped at the average age of 53 days. The probability of surviving from birth to 53 days was therefore taken to be $106/158 = .67$. This is equivalent to a monthly probability of surviving of .80. At the beginning of the breeding season of 1954, the 1953 cohort of young had become reduced to about 14 individuals. So, from age 53 days to the first breeding season (6.5 months), the probability of surviving was $14/106 = .11$, which is equivalent to a monthly probability of surviving of .73. It appears that the survival rate was greater in the hares before they began to be trapped (.80) than it was after they reached trappable age (.73).

Green & Evans (1940b) report the probability of surviving among hares from birth to the following February over a 7-year period. The rates were: 1932—.50 (approx.); 1933—.23; 1934—.29; 1935—.18; 1936—.12; 1937—.08; 1938—.91. On Bull Island the comparable rate from birth to the following February was $14/158 = .09$, approximately the same as the lowest (1937) rate in Minnesota.

The survival rate for young can be compared with that of the adult hares for the same period. From the mid-point of the breeding season to the following February, numbers of adults decreased from 42 to 13, a survival rate of .31. This is considerably higher than the rate of .09 for young hares. The Bull Island adults had a lower annual probability of surviving than the Minnesota hares. In Minnesota the adults maintained an almost constant annual survival rate (February to the following February) of .30 throughout the 7-year study. On Bull Island the corresponding rate was $13/58 = .22$. (The latter rate was probably actually lower than .22 because 58 is an underestimate of the number alive in February, 1953.)

The crude survival rate is defined as the number of hares of all ages alive in February divided by the number alive in the preceding February. On Bull Island there were 27 hares alive in February, 1954, compared with (more than) 58 alive in February, 1953. The crude survival rate is therefore $27/58 = .47$. In Minnesota the crude survival rates were: 1932-33—.48; 1933-34—.95; 1934-35—.69; 1935-36—.61; 1936-37—.21; 1937-38—2.28. The Bull Island rate falls between the two lowest Minnesota rates.

Predation. There is abundant evidence that predation was an important mortality factor on Bull Island. During the summer of 1953 an adult and an immature great horned owl were occasionally seen with snowshoe hare carcasses, and remnants of hares were often seen. Several owl pellets found on the island were composed of bones and fur of hares. Although sight records of owls were much less frequent before and after the summer of 1953, evidence appeared from time to time to indicate that owl predation is continuous on the island. Great horned owls or their signs have been observed on Bull Island every month except April and May. From June to November, 1953, owls were particularly common. Apparently an adult and one youngster were in residence on the island during that period.

A cursory examination of the owls' food habits was possible through analysis of regurgitated pellets. Apparently the owls in the area of the study do not have habitual roosting perches but scatter their pellets, few of which are found. Among 34 such pellets recovered, 15 contained remains of snowshoe hare, 6 contained unidentified birds (some of these pellets may have come from bald eagles), 4 contained pine squirrel, 4 contained longtail vole, 1 contained deermouse, and 4 contained unidentified material. This suggests that snowshoe hares may comprise nearly half (at least $15/34$) of the owl's diet. Twice, tags from marked hares were found in the pellets.

Craighead & Craighead (1956) found that great horned owls in Michigan and Wyoming consumed about 136 gm of food per day. On this basis, two owls would eat 48,960 gm of food in 180 days. If $15/34$ of the Bull Island owls' diet was snowshoe hare, this provides an estimate of 21,600 gm of hares eaten.

By the end of November about 160 hares had been born and about 135 of these had died. Approximately 20 of these were known to have died of causes not

related to the owls. At the same time about 25 adult hares died, of which about 5 were known to have died of causes unrelated to owls. Thus the total deaths possibly attributable to owls was 135. Since this total includes many more young hares than adults, it would appear that the average weight at death was less than half the adult size. If 500 gm is taken as an estimate of the average weight at death, the total weight of the 135 hares that died was 67,500 gm. Thus the 21,600 grams which the owls were calculated to have eaten accounts for approximately one-third of the total weight of the dead hares.

The proportion of hares killed by owls is probably greater than indicated above. The analysis was based on the assumption that only two owls were in residence on the island for six months. Owls were also there, though in less abundance, at other times. Also, on occasion there were more than two owls present. The carcass of a third owl, apparently killed by porcupine quills, was found on the island in August. The preponderance of evidence points to owl predation as the primary mortality factor. Of course, other factors such as disease and the cover-food relationships, may have affected prey vulnerability.

Besides the owl, the only other animal known to have killed hares on Bull Island was the mink. Apparently these killed only trapped hares. On four occasions hares were found killed and partly eaten in live traps, the evidence pointing to mink as the predators. Whenever such deaths occurred the hare traps were set and baited with the hare carcasses. Six mink were live trapped in this way from July 21 to August 21, 1953.

Judging from mink sign, such as tracks in the snow and droppings, it appears that the mink occur only transiently on the island. There is some evidence that they cruise across the lake using the islands across The Narrows as stepping stones. Signs were observed on Bull Island only in the months of March, April, May, July and August. There was no evidence that mink killed hares other than those in traps. Five mink scats found during the study consisted of insect remains only.

Of the several other potential or theoretical predators of hares on Bull Island (dogs, skunk, badger, bobcat, red-tailed hawk, osprey, bald eagle), none was implicated in the present study.

Disease and Parasites. The principal diseases encountered were "trap sickness" and ringworm. The only animal parasites encountered were ticks. A careful study of hare pathology might have revealed other diseases and parasites.

"Trap sickness," which is often encountered in live-trapped animals, has symptoms similar to those of shock disease (Green, Larson & Bell 1939). In this report the term "trap sickness" is used instead of shock disease because in the absence of pathological diagnosis it is not certain that the observed syndrome was identical to that defined by Green and his associates.

The symptoms of "trap sickness" ranged from very mild to severe. In their mildest form, the hares merely stopped to eat when released, instead of bounding away as they usually did. The more severe symptoms were intense and depraved hunger, followed by death. In the severest form, the hares died with the opisthotonic seizures typical of hypoglycemia. The symptom of "trap sickness" most often seen in the field was an increased appetite, sometimes accompanied by decreased wariness.

There appears to be considerable variation in the predisposition of individual hares to become afflicted with "trap sickness." Some hares showed symptoms the very first time they were caught. Others showed no symptoms even after repeated captures on consecutive nights. This may be evidence that the trapping *per se* may not be the cause of "trap sickness." Perhaps the illness is present prior to the trapping and is simply brought to the attention of the investigator through the trapping and incidental close observations of the hares.

Symptoms of "trap sickness" were first observed six days after trapping started on Bull Island. Hare No. 5, a male which had been captured previously on February 13 and 14, showed an excessive appetite and lack of normal cautiousness; upon release, it immediately spent about 20 minutes eating. Caught two more nights in succession, this hare died in the trap on February 18. In 18 months of trapping on Bull Island symptoms of "trap sickness" were observed in 28 of the 160 hares trapped. One death from "trap sickness" was observed. The following description is quoted from field notes. "6/19 [1953] 8:25 a.m. Hare 217-18 (Imm.) On release started eating pinegrass immediately—not even stepping out of the weighing sack. For 28 min. it ate—mostly *C. rubescens* but with the addition of one sprig of spiraea which I offered, and about 10 leaflets of *O. G.* [Oregon grape = creeping hollygrape]. Then at 8:15 it started sneezing, having just moved 10' away. The sneezing became acute at times with rapidly successive sneezes which sounded as if coming through much mucus in the nose. Once it wiped at nose with both front paws. At 8:27 it gave one short leap (about 1/2 length of body) fell on side, all feet quivered convulsively for 1± sec., head back legs extended. Heart not beating. No respiration. A minute later the heart beat steadily for 1± min. then stopped—no respiration. Rigor mortis occurred within 3 minutes. While eating in sack, hare urinated—probably normal amt. After death there is a small amount of soft feces at anus." Other hares were found dead in opisthotonic positions, most of them in the traps, occasionally free.

Apparently there was no effect of sex on incidence of "trap sickness." Of 159 hares captured in 1953, eighty-five were males and 74 were females, about an even division of sexes in the population. The incidence of trap sickness is also evenly divided between sexes—15 males and 13 females.

There appears to be some difference in incidence of the disease in the older and younger hares. Only three of the 58 adults trapped (5%) showed symp-

toms, while 25 of 101 young-of-the-year hares (25%) showed symptoms. These are significantly different ratios ($\chi^2 = 8.433, .01 > p > .001$). This is contrary to findings regarding shock disease by Green, Larson & Bell (1939). They concluded that "shock disease afflicts young and old hares in the proportions in which they occur on the Area."

There may be a seasonal variation in the prevalence of "trap sickness" (Table 21). From May to August, the prevalence of symptoms per capture was higher than it was the rest of the year. Since at this time of year most of the hares being captured were immatures, this may also reflect the effects of age.

The data presented in Table 21 also suggest that "trap sickness" may not occur in hares after their first breeding season starts. The only period when adults showed symptoms was from January to April. These four occurrences could have been young of the previous summer prior to (or coincident with) their initial breeding.

TABLE 21. The seasonal prevalence of "trap sickness" per snowshoe hare capture—by age groups.*

Season	NO. OF CAPTURES		SYMPTOM PER CAPTURE	
	Adult	Imm.	Adult	Imm.
January-February	75	0	.027
March-April	132	0	.015
May-June	98	47	.000	.106
July-August	70	197	.000	.071
September-October	12	56	.000	.036
November-December	25	72	.000	.042
Totals	412	372	.010	.065

* Young-of-the-year were considered adults after January 1 following the summer of their birth.

Ringworm was first reported as a disease of snowshoe hares in the present study (Adams, Salvin & Hadlow 1956). It is a fungus infection (*Trichophyton mentagrophytes*) which affects the epidermis, resulting in epilation, local matting of hair, and scalliness of the skin, and giving a "mangy" appearance.

Two kinds of ticks were found as ectoparasites of the hares on Bull Island—*Dermacentor andersoni* Stiles and *Haemaphysalis leporis-palustris* (Packard). No distinction was made between them in the field.

There was a marked seasonal variation in the incidence of ticks (Table 22). The ticks first appeared in March and reached a prevalence of infection of 100% in May when the number of ticks per hare reached the maximum range of about 50 to 150. In late August the incidence of infection and the number of ticks per hare decreased. By the end of October the hares were again free of ticks and continued so through the winter.

Numbers of ticks per infected hare were counted or estimated in the spring of 1953. In March 11 infected hares had an average of 5.4 ticks. In April the average for 19 hares was 23.0 ticks, and in May

TABLE 22. The prevalence of infection of hares by the ticks *Dermacentor andersoni* and *Haemaphysalis leporis-palustris*.

Month	NO. OF CAPTURES*		PREVALENCE**	
	1953	1954	1953	1954
January	..	43	..	0.0
February	30	5	0.0	0.0
March	18	20	94.4	40.0
April	19	20	100.0	90.0
May	13	23	100.0	100.0
June	72	0	100.0	..
July	56	14	100.0	100.0
August	169	..	98.8	..
September	29	..	62.1	..
October	38	..	10.5	..
November	84	..	0.0	..
December	13	..	0.0	..

* For which tick data were recorded.

** Prevalence is based on the number of infections per hare-capture rather than infections per hare. The prevalence percentage is practically the same in both cases

15 hares had an average of 81.6 ticks. Through the summer there were 50 to 150 ticks per hare.

Reports from other studies (MacLulich 1937, Green, Larson & Bell 1939, Severaid 1942, Seton 1953) indicate marked variations in kinds and numbers of ticks infecting hares. It appears from these reports that the Bull Island hares had a comparatively moderate to light level of infestation. Neither MacLulich (1937) nor Green, Larson & Bell (1939) considered ticks of causal significance in the population cycle.

Ticks from live-trapped hares were sent to the Rocky Mountain Laboratory to be tested for organisms of tularemia and Colorado tick fever. At the Laboratory the ticks were identified by Dr. Glen M. Kohls, and tested for Colorado tick fever by Dr. C. M. Eklund and for tularemia by Dr. J. Frederick Bell and Mr. John Moore. From May 15, 1953 to July 9, 1953, 53 collections were made from 29 adult and 11 immature hares. The ticks were identified as follows: *H. leporis-palustris*—67 adult ♂♂, 98 adult ♀♀, 7 nymphs; *D. andersoni*—119 adult ♂♂, 44 adult ♀♀, 1800 nymphs, 188 larvae. None of the *H. leporis-palustris* was tested for disease organisms. Of the *D. andersoni* 13 ♂♂, 16 ♀♀, 1,049 nymphs and 188 larvae were tested for tularemia only. The following numbers were tested for both Colorado tick fever and tularemia organisms: 173 ♂♂, 126 ♀♀, and 758 nymphs. No evidence of diseases was found.

During the study two deaths were observed to result from accidents.

Mortality factors have received much attention by many investigators. Criddle (1938) describes a changing picture of predation. Recently (1936) the wolves, coyotes and great horned owls hunted the hares and markedly reduced their numbers. Some survived in denser cover. Formerly this dense cover was hunted by the lynx and marten which are now scarce. Criddle (1938) also describes an unidentified disease which reduced hares from peak numbers to scarcity in a few months in 1923. MacLulich (1937) exhaustively re-

viewed theories and evidence concerning mortality and the ten-year cycle. He concluded that the cycle resulted from decimation by disease caused by the crowding which resulted from normal population increase. Which particular disease, parasite or combination would be the instrument of decimation he believed is a matter of chance. Severaid (1942) found coccidiosis common in his penned hares; he also found several other parasites and shock disease. Green and his associates found many disease agents but concluded that "shock disease" was the primary cause of the periodic die-offs (Green, Larson & Bell 1939).

There has been a strong tendency to consider shock disease as a universal single cause of cyclic die-off. A recent statement by some of those who worked on the Minnesota studies is therefore of interest (Philip, Bell & Larson 1955): "It is possible that a widespread decrease in the number of hares following peak abundance is due to a combination of environmental pressures such as disease, parasitism, and predation rather than to any single factor."

AMPLITUDINAL GRADATION IN POPULATION CYCLES

Lack (1954) lists four cardinal attributes of population cycles: (1) regularity of the peaks, (2) non-synchronous occurrence of peaks from place to place, (3) variability in the size of successive peaks at a given place, and (4) gradation in the amplitude of the cycle from north to south. While much has been written about cyclic regularity, little has been said, at least quantitatively, about amplitudinal gradation. In this section, the available information on gradation in snowshoe hare cycles is presented and discussed.

A. B. Howell (1923) pioneered in describing the existence of the north-south gradient. The huge population increases and spectacular die-offs of hares in the north are legendary. Preble (1908) quotes Major A. E. Snyder of the Royal Northwest Mounted Police reporting on snowshoe hare numbers in the vicinity of Whitehorse, Yukon, in 1907, "In a journey, recently, of twenty days' duration, I only saw two rabbits . . . where there were thousands two years ago." Seton (1953) considered hares scarce in northwestern Canada when there was one per sq mi, abundant when there were 1,000 and he remarks further that "I have seen as many as 10,000 to the square mile." MacLulich (1937) reported a shift in population density in Ontario from one hare per sq mi to 1,000 per sq mi.

Considerably smaller amplitudes have been reported in the more southern parts of the snowshoe hare's range. In Minnesota, Green & Evans (1940a) recorded a high: low ratio of 10:1 (539 per sq mi at the "high" of the cycle vs. 55 per sq mi at the "low"). In Wisconsin, using an index to snowshoe hare abundance obtained from state records of hunter kills, Grange (1949) found two cyclic "highs" to be respectively 5 and 2.5 times as large as the intervening "low." Brooks (1955), using a pellet counts to estimate the amplitude of fluctuations in West Virginia, reports a high which was 17 times larger than the preceding "low."

It appears that the amplitude of snowshoe hare cycles may vary from 1 to 1,000 or more in the north to as little as 1 to 2 or 3 in the South. However, recent studies cast some doubt on the validity, or at least on the simplicity, of the gradient concept. Using hunter kills, Buckley (1954) calculated that the "peaks" of several snowshoe hare cycles in Alaska were respectively 20, 12, and 3.4 times as large as the preceding or succeeding "low." In the Snowshoe Hare Enquiry, Chitty (1948) comments, "In the southern part [of British Columbia in 1943-44], although increase was reported by almost one-third of the observers, nearly two-thirds reported no change. These results confirm our previous conclusions that in this area there has been little apparent difference in numbers of rabbits in many years." This conclusion that there is no fluctuation contrasts with the results of the studies reported earlier, which indicate that cycles exist even in the most southern part of the hare's range.

Such differences in reports indicate the need for further information on the north-south gradient, with particular reference to amplitudinal variation within localities. Perhaps the nature of the gradient has been exaggerated by the occurrence of a few unusual but spectacular hare "plagues" in the north plus the difficulty of detecting the lesser fluctuations by casual observation. Most of the studies to date have been located in the northern United States and southern Canada (Fig. 12). Almost all of them have been made in, or close to, that portion of the snowshoe hare's range which is characterized by small-amplitude cycles. Some of these study areas occur on the margin of a transitional zone, between the southern area of low amplitude and the northern area of high amplitude, the existence of which is evident from a study of Butler's (1953) maps of the patterns of snowshoe hare cycles.

Dymond (1947) suggested that the uniform and simple environment (few alternative prey and predators) in the north, compared with that in the south, accounts for the greater cyclic variation. The gradient might also be explained in terms of a larger reproductive rate in the north (Christian 1950). The idea that cyclic increases are accompanied by increased productivity seems to have originated early in the consideration of cycles. MacLulich (1937) cites five authors from 1905 to 1924 who suggested that a correlation exists between cycles and litter size; the only concrete evidence presented was that of Preble (1908), who found that in a very small sample of pregnant females taken during the "low" of a cycle the number of embryos "seldom exceeded two." More recent information about the size and variation of litters in relation to cycles is summarized in Table 23. None of the more recent authors claims to have demonstrated any correlation between litter size and the cycle, and several (MacLulich 1937, Criddle 1938, Green & Evans 1940b) have denied the existence of a demonstrable correlation. While the evidence against appreciable variation in litter numbers is not so conclusive as that against variation in litter size, the earlier sec-

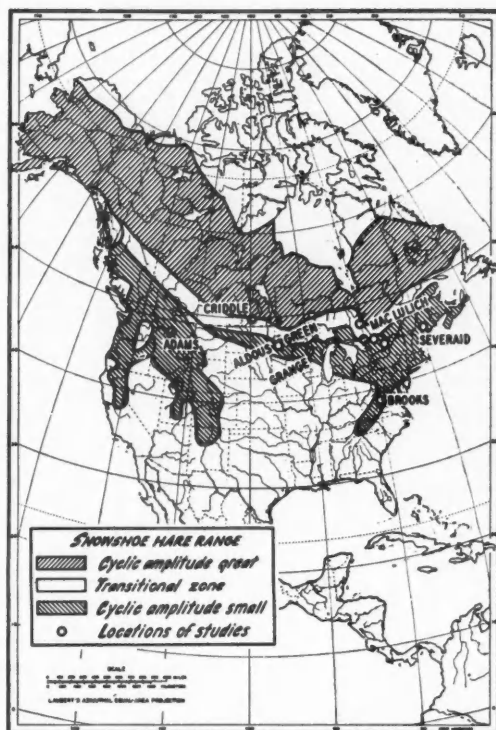


FIG. 12. The pattern of the amplitudinal gradient as indicated by the isoamplitudinal transition zone, and the location of the principal investigations of snowshoe hares, superimposed upon the range of the hares (after Hall 1951). (The four locations of Studies in Ontario all refer to MacLulich.)

tion of this paper which dealt with numbers of litters indicated that no striking differences were apparent. Unless new evidence can be produced to the contrary, productivity in snowshoe hares should be regarded as practically a constant, varying only within the limits of normal sampling error.

SUMMARY

A field study of an isolated population of snowshoe hares was conducted over an 18-months period on Bull Island in Flathead Lake, Montana. The geology, climate, vegetation, avian and mammalian fauna, and the history of the island and its environs are described. Methods of study included live trapping, field observations and studies of captive hares. The three main objectives were (1) to develop techniques for population censusing, (2) to analyze environmental factors affecting abundance and distribution of the hares, and (3) to study the general life history of the hares in comparison with similar studies elsewhere.

The census technique involved estimations of pellet numbers which were calibrated to hare numbers. Pellet numbers and hare numbers were determined by

TABLE 23. Average number of snowshoe hare young per litter in various localities.

	MEAN NO. EMBRYOS PER PREGNANCY (No. Pregnancies in Parentheses)							
	Manitoba		Ontario	Minnesota		Wisconsin	Maine	Montana
	Criddle (1938)	MacLulich (1937)	MacLulich (1937)	Green & Evans (1940b)	Aldous (1937)	Grange (1932)	Severaid (1942)	Adams
1923	L2.05(21)							
1924	L3.57(7)							
1925	3.11(18)							
1926	3.60(25)							
1927	4.38(8)					L2.00(2)*		
1928	3.83(6)							
1929	3.75(4)							
1930	3.83(6)					3.67(3)*		
1931	3.67(6)		3.50(2)		4.80(5)	3.00(1)*		
1932	2.50(16)		3.33(3)	3.17(23)	3.13(?)			
1933	H3.71(21)	4.00(27)	H2.75(20)	H3.58(12)	H3.11(?)			
1934	4.27(11)			2.79(34)	2.77(?)			
1935	3.75(4)			2.54(35)	2.65(?)			
1936				3.05(20)				
1937				2.64(11)				
1938				L3.20(5)				
1939							2.86(28)*	
1940							H2.89(53)*	
1941							2.96(80)*	
1953								2.72 (32)
1954								3.00 (9)

* Born in captivity.

H The year indicated by the author as the "high" of the cycle.

L The year indicated by the author as the "low" of the cycle.

plot sampling and by live-trapping respectively. Then the ratio of pellets to hares per day was calculated. Two kinds of analysis were used in estimating hare numbers. By the recapture method the calibration coefficient for pellet numbers was 481 pellets per hare-day. By the calendar-graph method, the coefficient was 554 pellets per hare-day.

Three kinds of environmental factors were analyzed in their relation to hare distribution and abundance—the food-cover-predator complex, cover density, and physical obstacles. In the food-cover-predator complex the hares leave protective cover where food is scarce to obtain food in the more open parts of their habitat. This increases their vulnerability to predation, particularly to great horned owls. Response to cover density was measured by pellet abundance under light to heavy cover. Pellet numbers increased with cover density through four classes of density, but decreased at the heaviest density—possibly because the cover was too dense to permit any food plants to grow there. Quantitative studies of pellet abundance in relation to physical obstructions revealed no appreciable effect of the latter.

The breeding season extended from late February to early July in males and from mid-March to early July in females. Lactation was practically continuous from late April to late September. There was an average of about 2.9 pregnancies per female in 1953. In 1954 the average was about 2.8 litters. The average number of young per litter was about 2.6 in 1953, 3.00 in 1954.

At birth the hares weighed an average of 40 grams,

average weight at maturity was 1,000 to 1,100 grams. Hares born in early summer nearly completed their growth by fall and grew little during the winter. Hares born later continued to grow during their first winter.

The sex ratio did not differ significantly from 1:1 in either adults or young of 1953. Apparent variations from the even ratio occur as a result of seasonal sex variations in response to trapping. More males were caught from February to April. More females from May to August.

Adult hares were distinguishable from young of the year by the color of their feet and, in females, by palpability of teats. Until the fall molt 93% of the young hares had all gray feet. All adults had some white on their feet. During the winter 1953-1954 all but one of nine adult females (had bred during 1953 breeding season) had palpable teats, all but one of sixteen young (born in 1953) did not have palpable teats. The ratio of adults to the young of 1953 was about 1:1 in February, 1954.

The home ranges of individuals was largest for adult males (25 acres), second largest for adult females (19 acres) and smallest for immature hares (14 acres). Values given for range size are minimal. Only the range of adult males was significantly different. There was much overlapping of home ranges. Dispersal movements outside the home ranges occurred in males only, though in both adults and young. Territoriality seemed to be exerted in the area around the individual itself. Hares rested in forms, sometimes using a resting place only once, sometimes repeatedly.

Two or more hares occasionally used the same form, but never at the same time.

Hares rely on protective coloration and immobility or on flight for protection. Flight is increasingly preferred as the animal matures. Occasionally hares ran into burrows when chased.

Twenty-one species of plants used as food by hares are listed by relative amounts eaten, season of use, and parts eaten. Reingestion is described as observed in the field.

Mortality is analyzed in terms of probability of survival, q ($= 1 - \text{probability of dying} = \text{number alive at one time divided into a number alive at a later time}$). From birth to average time of first capture (53 days) $q = .67$. The equivalent monthly $q = .80$. From the time of first capture to the following February just prior to the breeding season (6.5 months) $q = .11$, equivalent monthly $q = .73$. From birth to the first breeding season, monthly $q = .09$, which is similar to the lowest survival rate found during the crash in Minnesota.

Survival rate for adults from the average time of birth of young to the following February is .31 compared with .09 for young hares. The annual probability of survival for adults was .22 compared with .30 in Minnesota.

The crude survival rate from the start of the 1953 breeding to the same time in 1954 was .47, almost as low as the Minnesota hares at the height of their crash.

Several causes of mortality and morbidity were observed. Great horned owls were the main predators, accounting for at least one-third of all deaths. Mink killed a few hares in traps. The principal diseases were "trap sickness" and ringworm. Symptoms of "trap sickness" are depraved and ravenous appetite, loss of wariness, opisthotonic seizures and death. Twenty-eight of the 160 hares trapped showed symptoms of this disease. It affected both sexes but more young hares (25%) than adults (5%). Ringworm (*Trichophyton mentagrophytes*) was discovered for the first time in snowshoe hares in the present study. Ticks were present in relatively small numbers (50-150 ticks per hare) on the hares in summer and were not considered to be of significance. Ticks gave negative tests for tularemia and Colorado tick fever.

Amplitude of cycles varying from 1:1,000 to 1:2.5 were reported in several comparable studies of snowshoe hares. Although the amplitude appears to be greater northward over the hare range, the north-south gradient is somewhat obscured by amplitudinal variation within localities.

LITERATURE CITED

- Adams, L., S. B. Salvin & W. J. Hadlow. 1955. Ringworm in a population of snowshoe hares. *Jour. Mammal.* 37: 94-99.
- Aldous, C. M. 1937. Notes on the life history of the snowshoe hare. *Jour. Mammal.* 18: 46-57.
- Anonymous. 1952. Climatological Data, Montana. U. S. Weather Bureau 55: 206-217.
- . 1953. Climatological Data, Montana. U. S. Weather Bureau 56: 1-209.
- Brooks, M. 1955. An isolated population of the Virginia varying hare. *Jour. Wildl. Mgt.* 19: 54-61.
- Buckley, J. L. 1954. Animal population fluctuations in Alaska—a history. *Trans. 19th No. Amer. Wildlife Conf.* 19: 338-357.
- Burt, W. H. & R. P. Grossenheider. 1952. A field guide to the mammals. Boston: Houghton Mifflin Co. xxiv + 200 pp.
- Butler, L. 1953. The nature of cycles in populations of Canadian mammals. *Canad. Jour. Zool.* 31: 242-262.
- Chitty, H. 1948. The Canadian snowshoe hare enquiry. 1943-1946. *Jour. Anim. Ecol.* 17: 39-44.
- Christian, J. J. 1950. The adreno-pituitary system and population cycles in mammals. *Jour. Mammal.* 31: 247-259.
- Craighead, F. C. & J. Craighead. 1956. Hawks, owls and wildlife. Harrisburg, Pa.: Stackpole Co. xix + 443 pp.
- Criddle, S. 1938. A study of the snowshoe rabbit. *Canad. Field Nat.* 52: 31-40.
- Daubenmire, R. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. *Ecol. Monog.* 22: 301-330.
- . 1953. Classification of the conifer forests of eastern Washington and northern Idaho. *Northwest Sci.* 27: 17-24.
- Davis, D. E. 1953. Analysis of home range from recapture data. *Jour. Mammal.* 34: 352-358.
- . 1955. Social interaction of rats as indicated by trapping procedures. *Behavior* 8: 335-343.
- Davis, R. J. 1952. Flora of Idaho. Dubuque, Iowa: Wm. C. Brown Co. iv + 828 pp.
- Dice, L. R. 1923. Mammal associations and habitats of the Flathead Lake Region, Montana. *Ecology* 4: 247-260.
- . 1952. Natural communities. Ann Arbor: Univ. Mich. Press. x + 547 pp.
- Dymond, J. R. 1947. Fluctuations in animal populations with special reference to those of Canada. *Roy. Soc. Canada Trans.* 41: 1-34.
- Grange, W. B. 1932. Observations on the snowshoe hare, *Lepus americanus phaeotus* Allen. *Jour. Mammal.* 13: 1-19.
- . 1949. The way to game abundance. New York: Charles Scribner's Sons. xvii + 365 pp.
- Green, R. G. & C. A. Evans. 1940a. Studies of a population cycle of snowshoe hares on the Lake Alexander area. I. Gross annual censuses, 1932-1939. *Jour. Wildl. Mgt.* 4: 220-238.
- . 1940b. Studies of a population cycle of snowshoe hares on the Lake Alexander area. III. Effect of reproduction and mortality of young hares on the cycle. *Jour. Wildl. Mgt.* 4: 347-358.
- Green, R. G., L. C. Larson & J. F. Bell. 1939. Shock disease as the cause of the periodic decimation of the snowshoe hare. *Amer. Jour. Hyg.* 30: 83-102.
- Green, R. G., L. C. Larson, J. F. Bell & C. A. Evans. 1938. The effect of shock disease on the weights of

- snowshoe hares. Minnesota Wildlife Disease Investigation Reports 4: 52-55. Processed.
- Hall, E. R. 1951. A synopsis of the North American Lagomorpha. Univ. Kans. Publ. Mus. Nat. Hist. 5: 119-202.
- Howell, A. B. 1923. Periodic fluctuations in the numbers of small mammals. Jour. Mammal. 4: 149-155.
- Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press. xviii + 343 pp.
- MacLulich, D. A. 1937. Fluctuations in the numbers of the varying hare (*Lepus americanus*). Univ. Toronto Studies, Biol. Ser. 43: 136 pp.
- Nelson, E. W. 1909. The rabbits of North America. U. S. Dept. Agric., Bureau of Biological Survey, North American Fauna 29. 314 pp.
- Philip, C. B., J. F. Bell, & C. L. Larson. 1955. Evidence of infectious disease and parasites in a peak population of black-tailed jack rabbits in Nevada. Jour. Wildl. Mgt. 19: 225-233.
- Preble, E. A. 1908. A biological investigation of the Athabaska-Mackenzie region. Bureau of Biological Survey, North American Fauna 27: 1-574.
- Seton, E. T. 1953. Lives of game animals. Vol. 4, Pt. 2. 441-949.
- Severaid, J. H. 1942. The snowshoe hare, its life history and artificial propagation. Maine Dept. Inland Fisheries and Game. 95 pp.
- . 1945. Breeding potential and artificial propagation of the snowshoe hare. Jour. Wildl. Mgt. 9: 290-295.
- Stickel, L. F. 1954. A comparison of certain methods of measuring ranges of small mammals. Jour. Mammal. 35: 1-15.
- Watson, J. S. & R. H. Taylor. 1955. Reingestion in the hare *Lepus europaeus* Pal. Science 121: 314.
- Webb, W. L. 1937. Notes on the sex ratio of the snowshoe rabbit. Jour. Mammal. 18: 343-347.

RESPONSE OF TRUE PRAIRIE VEGETATION ON MAJOR FLINT HILLS RANGE SITES TO GRAZING TREATMENT

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INTRODUCTION

Native prairie has been the home of grazing animals for untold centuries. Prairie plants are eminently adapted to grazing, and moderate grazing use is not detrimental to their development. Climax grassland, when properly grazed, retains essentially its natural composition. Yet, when livestock are placed on range too early in the season, when they are left there too long, or when too many animals are confined to an area, grazing becomes so excessive that normal plant cover cannot be maintained. Numerous changes in the vegetation then occur. The rate at which these changes take place depends on the degree of abuse. They sometimes take place so gradually that deterioration may not readily be recognized until the plant cover has been greatly modified, but when prairie is grazed intensively major changes may occur within a few years.

Native grassland still occupies some 2,800,000 acres of the 4 million-acre Flint Hills region of Kansas lying principally in the 30- to 38-in. rainfall belt between the 96th and 97th meridians as shown in Fig. 1. The Flint Hills area supports a year-round cattle population of perhaps 500,000 head plus some 300,000 additional ones shipped there each year to graze during summer. Utilization of bluestem range pastures has traditionally been through summer grazing by cattle, the period of heaviest use corresponding with

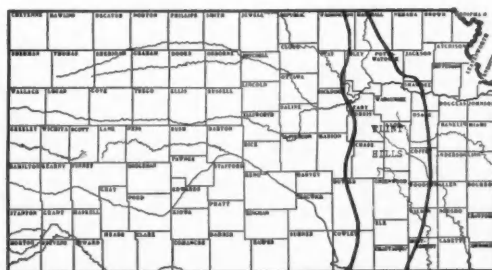


FIG. 1. Approximate (generalized) boundaries of the Flint Hills grazing area of Kansas.

that of the three months of most rapid grass growth, May, June, and July. Cattle often remain until fall, and some bluestem pastures are stocked year-long. Much of the Flint Hills remains in good to excellent range condition because of the nature of the grazing management. Transient cattle are grazed each year during the period of rapid vegetative growth and marketed in time for the range grasses to make sufficient top growth for adequate storage of root reserves.

The native vegetation of the area is classified as true prairie, dominated by little bluestem (*Andropogon scoparius*)³ and big bluestem (*A. gerardi*) to-

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³ Scientific names of grasses according to Hitchcock, A.S., U.S.D.A. Misc. Publ. 200, Rev. 1951, and of other plants according to Gates, F. C., The Flora of Kansas. 266 pp. Kansas Agric. Exp. Sta. Publ., 1940.

gether with several less abundant grasses of similar growth habit. Small amounts of short grasses occur, particularly on preclimax sites, while forbs, although often conspicuous at flowering time, seldom constitute a large portion of the climax vegetation. Sedges and rushes make up a small percent of the plant cover.

The history of range utilization in the Midwest has been one of exploitation followed by depletion of the vegetation. Aldous (1938) pointed out that there had been a steady decline in the grazing capacity of bluestem pastures in Kansas. "Prior to 1900 most of the pastures were stocked at the rate of two acres for a cow or mature steer. The average has been gradually decreased until in 1933 the best pastures were carrying one mature animal to four acres, while the average for the bluestem region as a whole was five acres per head for the summer grazing period." This has further declined in recent years until the best pastures now carry on the average only one animal unit per 5 acres or more.

Grazing use is the major factor affecting range conditions. The chief criterion for detecting and evaluating trend in range condition is change in species composition. Since quantitative data on the course of such change in Flint Hills bluestem grassland have not generally been available, a study of the effects of different grazing treatments on the vegetation and on the livestock was initiated in 1949 on typical bluestem range to provide such data.

CLIMATE AND PHYSIOGRAPHY

The climate conditions of the Flint Hills are typical of true prairie. Average annual precipitation varies from 30 in. in the northwestern part to 38 in. in the southeastern part of the region. About 75% of the moisture falls during the growing season, which ranges in length from an average of 170 days in the north to 190 days in the south.

Elevations vary from 1,500 ft in the central part of the region to 850 ft at its southeastern extremity. Physiographically a strongly dissected plain, the terrain is rolling to hilly with relatively smooth, narrow divides bordered by rock outcrops and steep slopes. Escarpments occur adjacent to major stream valleys.

The residual soils have developed from massive limestones, interbedded gray and yellow shales, and highly flinty or cherty limestones of the lower Permian formations (Fly 1946). Under the native bluestem vegetation the soils throughout the Flint Hills have developed dark, well-granulated silt loam or silty clay loam surface horizons. Texture and consistency of subsoil, depth of soil, and degree of stoniness vary widely with the character of the parent material and the degree of slope. Broken rock and chert allow moisture and plant roots to penetrate deeply. However, wide variations exist in the ability of the soils to support the regional climax type of vegetation. The surface soils are slightly acid in reaction and the fertility is moderate to high.

VEGETATION-SOIL RELATIONSHIPS

A study by Anderson & Fly (1955) of the relationship of the native plant population to soil differences on this experimental area revealed a number of distinct vegetation-soil units that were recognized as range sites. Six such sites were recognized and shown to be representative of broad areas of Flint Hills range. Major range sites occurring on the experimental area are outlined in Fig. 2. In the present study, comparisons have been made within these range sites and among grazing treatments.

Ordinary Upland Range Site. Lands having sufficient depth of soil with medium or loamy texture and hence with suitable soil-plant-moisture relations to support the type of vegetation that is climax on the zonal soils of the regional climate.

Limestone Breaks Range Site. Lands similar to the above but occurring on slopes of 35% or more and therefore subject to somewhat greater loss of moisture by runoff when closely grazed, and with less development. The vegetation, however, is like that of the above site in its major features and may be considered climax in nature.

Clay Upland Range Site. Lands having sufficient depth of soil but with somewhat less infiltration, slower permeability, and a smaller percentage of water available to plants than ordinary upland, hence supporting a somewhat preclimax vegetation.

Claypan Range Site. Lands having sufficient depth of soil, but with even more restrictive water relations than the clay upland sites, thus supporting a preclimax vegetation.

Very Shallow Range Site. Lands having insufficient depth of soil for normal water storage, hence supporting under proper grazing a vegetation distinctly preclimax.

Lowland Range Site (gullied). Lands receiving more water than normal and having, because of position and soil depth, such moisture relations as to



FIG. 2. Distribution of major range sites in typical Flint Hills range. Shown here are pasture 3 (light stocking) at the left and pasture 2 (heavy stocking).

- OU = Ordinary upland
- LB = Limestone breaks
- CU = Clay uplands
- Ld = Lowland (gullied)

support a post climax vegetation under proper grazing (with gullies controlled).

GRAZING EFFECTS ON VEGETATIONAL COMPOSITION

The grazing season in Flint Hills bluestem pastures usually begins about the time the dominant grasses begin to show spring growth and sometimes even earlier than this. Anderson (1951) pointed out that at that early date animals feed on cool season species such as prairie junegrass (*Koeleria cristata*), Kentucky bluegrass (*Poa pratensis*), and certain forbs. Weaver & Darland (1948) have shown that grazing use in similar grassland shifted to species of the bluestem type as soon as they were a few inches tall and that under heavy stocking these prairie species were repeatedly grazed until late fall. This resulted in a change in species composition away from the prairie dominants toward such pasture grasses as Kentucky bluegrass. Such an increase in Kentucky bluegrass was observed by Anderson (1940) to be widespread in the Flint Hills prior to the great drought of the 1930's, but this invading species practically disappeared in the extremely dry season of 1934.

CLASSIFICATION OF RANGE PLANTS

The task of maintaining natural grazing land is based upon a knowledge of the vegetation and its ecology. Most climax dominants and certain minor species of the true prairie, including many forbs, decrease under close grazing, but others members of the climax increase to take their place. If grazing pressure continues, the latter also begin to decrease, and invasion by weeds takes place. These responses were recognized by Smith (1940) who called attention to the fact that prairie species were forced out by grazing in the order of their palatability or edibility. Weaver & Hanson (1941) described stages of range deterioration from climax to depletion, classifying prairie species into 6 groups based on response to grazing. Decreasing, increasing, and invading grasses and forbs were listed. Dyksterhuis (1949) showed that degrees of grazing disturbance in grassland could be measured quantitatively by comparing the current relative coverage or production with that of the climax as determined by careful study of prairie relicts on the same kind of soil. Percentages of decrease, increase, and invaders were established as the basis for measuring degeneration.

The major decreaseers in Flint Hills range include big bluestem, little bluestem, and indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and others. Major increaseers include Kentucky bluegrass (an invader that has become naturalized and behaves in most respects as an increaseer), sidecoats grama (*Bouteloua curtipendula*), blue grama (*B. gracilis*), hairy grama (*B. hirsuta*), buffalograss (*Buchloe dactyloides*), tall dropseed (*Sporobolus asper*), pen sedge (*Carex pensylvanica*), and baldwin ironweed (*Vernonia baldwini*). Among the major invaders are annual bromes (*Bromus* spp.), little barley

(*Hordeum pusillum*), sixweeks fescue (*Festuca octoflora*), western ragweed (*Ambrosia psilostachya*), wavyleaf thistle (*Cirsium undulatum*), hoary vervain (*Verbena stricta*), and curlycup gumweed (*Grindelia squarrosa*).

DROUGHT EFFECTS ON VEGETATION COVER

There is a close relationship between forage production and annual precipitation. Savage (1937) observed that on the Great Plains the drought of 1933-1934 caused a decline of 65% in basal area of major grass species on ungrazed plots. Weaver (1954) showed that in true prairie areas moderately affected by the drought of the 1930's spaces bare of living plants were more or less isolated. Open spaces were plentiful where drought had been more severe and formed an irregular network of unoccupied soil surface. The cover was so decimated in some places that terrain appeared almost bare throughout the summer of the following year. The more mesic little bluestem, indiangrass, and Kentucky bluegrass had disappeared from some areas, and only blue grama, sidecoats grama, and certain xeric forbs remained. The major species to increase with the drought were western wheatgrass, buffalograss, blue grama, and six-weeks fescue.

Drought damage to plants may be affected materially by grazing use. Studies by Craddock & Forsling (1938), Nelson (1934) and Savage (1937) indicated that conservative grazing is little or no more harmful than total protection. Heavy grazing decreases both the depth to which roots penetrate and the volume of root production, hence overgrazed plants suffer great damage from drought. Savage (1937) found that decreases in production of the principal grasses of the Great Plains under drought conditions were directly proportional to the intensity of grazing.

DEFERRED-ROTATION GRAZING

Deferred-rotation grazing involves the division of a range into several units, one or more of which is deferred each year. Deferment allows plants on the protected areas to reach a stage of growth before grazing that will permit a substantial increase in plant food reserves and in some instances, seed production. Experiments have shown that increased grazing use can safely be practiced following deferment. Sarvis (1923), comparing a deferred-rotation system with season-long grazing of different intensities in the northern Great Plains, found that 7 acres were required to supply enough forage for one steer and yet maintain the forage cover under season-long grazing. From 4 to 5 acres per steer per season were enough when deferred-rotation grazing was practiced.

Studies in Colorado by Hanson, Love & Morris (1931) showed that 9 yrs of deferred-rotation grazing resulted in a 53% increase in density of vegetation, while the total number of undesirable plants actually decreased 18%.

Stoddart & Smith (1943) summarized the advantages of deferred-rotation grazing as follows: (1) in-

creased vigor of plants, resulting in more rhizomes, tillers, roots, and foliage, (2) increased seed production, (3) seedlings established more easily, (4) reduction of trampling, (5) maximum forage yield attained under full stocking, and (6) range improvement and other benefits ordinarily accompanying stock reduction can be obtained without curtailing stocking.

Anderson (1951) called attention to an additional benefit from deferred grazing that often is not recognized, the improved distribution of livestock over the range. Deferment requires that the range be divided somewhat by cross fencing, and this gives better control of livestock distribution. It has been shown that improper distribution of grazing animals may be a serious factor in range deterioration, often resulting in severe overgrazing of some parts of the range and underutilization of others (Brinegar & Keim 1942; Stoddard & Smith 1943).

HERBAGE YIELDS AS A RANGE INDICATOR

Increase in dry matter probably is the best single measure of forage production (Hanson 1950). Ahlgren (1947) reported that clipping or mowing ungrazed plots or protected areas in pastures probably is the most common procedure used in measuring the results of pasture management research. It is particularly suited to trials which include a large number of variables and may give more precise yield estimates than those based on animal productivity and maintenance. Using movable cages, Nevens (1945) showed that the difference between the weight of clipped herbage produced within plots protected from grazing and of that remaining after grazing and then clipped was a measure of the quantity consumed by the livestock.

MATERIALS AND METHODS

The study reported here was designed to evaluate the response of true prairie vegetation on major Flint Hills range sites to grazing treatment. The treatments compared were heavy, moderate, and light season-long stocking and deferred-rotation grazing at the moderate stocking rate. The results are reported in terms of vegetational responses by range sites. Major emphasis is on species composition and on trends that have developed under the different treatments. Herbage and mulch yields are also given.

EXPERIMENTAL AREA

The pastures in this study are typical Flint Hills grasslands, located 5 mi. northwest of Manhattan, Kansas. The vegetation is predominantly true prairie, with big bluestem, little bluestem, and indiangrass making up at least 50% of the vegetation on climax sites. Kentucky bluegrass has invaded the entire area.

GRAZING TREATMENTS

Six pastures of 60 acres each were included in the trials. Three of these were grazed season-long (May 1 to approximately the end of October) and 3 in a

deferred-rotation plan. Season-long grazing was at 3 stocking rates, 3.75 acres per animal unit⁴ (pasture 2), 5.0 acres per animal unit (pasture 1), and 7.5 acres per animal unit (pasture 3). These will be referred to as heavily, lightly, and moderately stocked pastures, respectively.

The 3 pastures in the deferred-rotation group (pastures 4, 5, and 6) were stocked on the average at the same rate as pasture 1. All of the animals were placed on two of the pastures during May and June while the third was being deferred. On approximately July 1 all these animals would be shifted to the deferred pasture in order to use the grass quickly and to allow summer protection of the two pastures grazed earlier. Toward fall, if the grass became short under this intensive summer use, the gates would be opened to allow free access to all 3 pastures. This treatment was rotated annually among the three pastures of the group so that the over-all average stocking rate was 5 acres per animal unit.

Stocking has been with yearling steers, each considered to equal approximately $\frac{2}{3}$ of one animal unit. Five acres per animal unit for the 6 months beginning May 1 is considered moderate stocking for the Flint Hills.

SAMPLING METHODS

Botanical composition and density were studied by means of plant census data obtained from randomized line transect samples as described by Canfield (1941) and Parker & Savage (1944) and adapted by Anderson (1942) to bluestem vegetation. The transects were not located permanently but were randomized each year. Approximately 75 such samples were taken each year in each 60-acre pasture. Each line sample was 10 m in length, and since it was assumed that an area 1 cm wide was sampled, each sample was considered to have an area of 1000 sq cm. All live vegetation with its basal portion beneath the line and all upright culms touching either side of the line were measured and counted. Where the line passed through a clump of vegetation the diameter of the clump directly under the line was measured in centimeters along the line. Where a single culm touched the line it was considered to occupy 1 sq cm. The samples were taken in June and July each year. Each sampling location was marked on an aerial photograph of the area.

Clipping samples were taken at the close of the 1953, 1954, and 1955 growing seasons to measure the top growth and mulch remaining. Ungrazed samples were obtained in 1955 by placing cages at randomized points on the 3 major range sites at the beginning of the grazing season. The cages were constructed of number 10, 48-in. woven wire, each covering an area four feet square. Approximately 10 samples were taken each year in each major range site (ordinary upland, limestone breaks, and clay upland) per pasture.

⁴ An animal unit in this trial is defined according to Vinal, H. N. & A. T. Semple. Jour. Amer. Soc. Agron. 24: 836-7. 1932.

Clippings were taken at the close of the growing season within a metal frame 25.04 in. square (1/10,000 acre). One clipping was taken under each cage and another adjacent to it. All the vegetation within the metal square was clipped at a uniform height as near soil level as possible. Unpalatable forbs were separated from the forage in the field in 1954 and 1955 since it had been found by Herbel (1954) that weighing unpalatable forbs with the forage confounded the results. All of the mulch within the metal square was also collected so that there was a sample of forage, unpalatable forbs, and mulch from each sampling area. Each was air-dried and weighed.

EXPERIMENTAL RESULTS

LINE TRANSECT DATA

Perennial grasses have averaged approximately 80% of the basal cover, but only two species, big bluestem and little bluestem, were present in quantities averaging above 10% each. Three species, indiagrass, sideoats grama, and Kentucky bluegrass, each averaged between 5 and 10% of the basal cover. These 5 grass species plus the sedges and rushes were the only ones present in sufficient quantity to permit statistical analysis. Statistical analyses were also calculated for total decreasing species of grasses, total increasing species of grass, total perennial grasses, total perennial forbs, and total vegetation. Total decreaseers analyzed as a group in this study included big bluestem, little bluestem, indiagrass, switchgrass, prairie junegrass, and prairie dropseed (*Sporobolus heterolepis*), while total increasing species of grass included sideoats grama, buffalograss, Kentucky bluegrass, blue grama, hairy grama, purple lovegrass (*Eragrostis spectabilis*), tumblegrass (*Schedonnardus paniculatus*), windmillgrass (*Chloris verticillata*), and sand dropseed (*Sporobolus cryptandrus*), scribner panicum (*Panicum scribnerianum*), and tall dropseed. Total perennial grasses include both groups plus traces of other less abundant ones not reported separately. Annual grasses, annual forbs, and shrubs made up such small portions of the plant cover that they were not analyzed statistically.

Only 3 range sites, ordinary upland, limestone breaks, and clay upland occurred in areas large enough in all 6 pastures to permit adequate sampling for statistical analyses. Since the grazing treatments began in 1949, statistical analyses were computed on the 1950 through 1955 data. The statistical treatment consisted of separate analyses of variance for the 11 species or groups of species for each of the 6 yrs and each of the 3 major range sites. Analyses of variance for each year showed how the species behaved each season under the various treatments. Annual behavior is important in interpreting trends. In addition, trends were calculated for nine of the species or groups of species over the 6-year period in each of the major range sites. Analyses of variance were also calculated for the 11 species or groups of species for each of the 3 sites on the 1947 popula-

tion sampling data to determine the degree of homogeneity among pastures.

All statistical analyses were calculated on actual numbers of culms or the square centimeter basal coverage of a species or a group of species per 10-m line transect. Thus, any changes or significant differences indicated by the statistical analyses apply directly to changes in density or basal coverage. Since percentage of total vegetation instead of basal cover is commonly used in range condition estimates, a separate study of such percentages is also included for each of the major species and groups of species.

1947 Data. The grazing treatments on all the pastures except pasture 3 began in 1949. Pasture 3 was deferred in 1949 and thereafter grazed season long each year at the light stocking rate. The experimental area had been uniformly grazed as a single large pasture prior to fencing in 1948. An analysis of variance on data taken in 1947 on each of the above mentioned species or groups of species showed that in only 8 of the 33 vegetation-range site combinations were there significant differences.

Natural vegetation usually shows much variability, and some of the important differences found in 1947 remained through several years of sampling. Using least significant differences it was found that before the trials were started ordinary upland had significantly more big bluestem in what became the heavily grazed pasture than in the pastures later stocked moderately. This carried over throughout the sampling period (1950-1955). Similarly, Kentucky bluegrass on ordinary upland in pasture 5 of the deferred group ranked high in most years. The lightly stocked pasture ranked high in sideoats grama in its limestone breaks range site at first but this increaser gradually declined. The clay upland site in the lightly stocked pasture was high in increasing species of grass in most years. Because of its location, animals tended to congregate on this site and to utilize it closely. The other differences noted above did not seem to influence subsequent sampling.

Total Decreasers. In summarizing range plant populations, certain species have been grouped as decreaseers because they diminish in abundance under heavy grazing use. Average basal areas of total decreasing species of grasses in square centimeters per 10-m line transect were studied each season on each range site by means of analysis of variance and regression coefficient. Decreasing grasses as a group declined in the three major range sites during the 1950-55 period. Average declines did not differ significantly among grazing treatments except in the limestone breaks site where the moderately stocked pasture had a significantly greater decline than all the other pastures except the lightly stocked one. Some significant differences occurred within certain seasons. For example, the decreaseers had become significantly less abundant in ordinary upland, limestone breaks, and clay upland in the heavily stocked pasture, but general declines due to the drought tended to obscure this by 1955. Some-

what similar trends were noted for the moderately stocked pasture, although in the clay upland site striking declines continued in this pasture. In the very shallow site there was a reduction in quantity of total decreasers in all pastures over the six-year period, the overstocked pasture having the smallest number in 1954 and 1955. This group of grasses has also declined on the claypan site.

Relative quantity of decreasers is an important measure of range condition. Percentages of decreasers for the years 1950 through 1955 for all range sites are presented in Table 1. In the ordinary up-

TABLE 1. Total decreasers. Percentages in the total plant cover for 1950-1955 for all of the range sites.

Range site	Pasture No.	YEARS					
		1950	1951	1952	1953	1954	1955
Ordinary upland	1	68.9	65.2	60.3	61.4	58.4	56.2
	2	60.3	58.2	55.2	49.5	35.9	29.1
	3	54.6	63.2	59.6	62.2	52.6	53.1
	4	67.8	59.9	54.0	59.4	51.5	45.8
	5	63.4	70.1	60.8	57.8	53.6	44.9
	6	63.5	63.1	64.0	68.7	59.5	42.3
Limestone breaks	1	67.2	67.7	65.0	57.2	51.5	46.4
	2	62.9	51.8	60.8	54.5	51.4	44.6
	3	58.6	55.6	68.9	74.8	74.3	70.2
	4	70.0	61.6	76.1	70.8	69.1	65.4
	5	64.6	70.1	75.0	79.2	71.4	65.9
	6	69.2	69.7	71.2	71.1	69.9	67.1
Clay upland	1	54.7	53.5	42.9	46.4	27.2	13.1
	2	32.1	44.2	42.9	30.3	22.3	29.7
	3	31.8	51.5	46.3	44.3	30.6	21.2
	4	49.3	52.1	52.2	46.0	39.0	21.4
	5	47.9	56.6	54.1	46.7	40.0	26.5
	6	40.9	55.6	55.2	61.1	37.7	40.6
Very shallow	1	71.0	42.9	50.7	52.5
	2	14.7	30.9	27.2	34.9	19.4	7.9
	3	42.6	46.9	41.0	32.4	18.7	24.3
	4	64.5	40.6	38.0	22.1	15.7
	5	77.1	61.2	72.1	61.8	37.2	31.8
	6	49.6	27.5	40.4	13.3
Claypan	4	18.1	32.9	26.4	19.1	21.8	10.6
	5	17.4	15.5	0.9	15.2	10.7

Pasture 1 moderately stocked, pasture 2 heavily stocked, pasture 3 lightly stocked, and pastures 4, 5, and 6 grazed in a deferred-rotation system.

land range site there has been a relative decline in all pastures, particularly the heavily stocked one. In limestone breaks there has been a marked decline of decreasers in pastures stocked moderately to heavily, a slight increase in the lightly stocked pasture, and no important change in deferred pastures. In clay upland this group of grasses has suffered a sharp percentage decline in the pasture stocked moderately and a slight to moderate decline in the others. The pasture stocked heavily actually showed an increase in the percentage of decreasers in 1955 when compared to 1954 but, as shown later, this resulted from the sharp drop in quantity of Kentucky bluegrass in this site in this pasture. In the very shallow range site there has been wide fluctuation in

relative cover of total decreasers, most pastures showing a decrease. These grasses have also declined in the claypan range site.

Big Bluestem. This grass has high palatability or grazing preference and is selected by livestock even where other forage is abundant (Weaver & Tomanek 1951). It is the most abundant and most important tall grass in the true prairie. Big bluestem and little bluestem together may constitute 50% or more of the plant cover. Big bluestem fluctuated but little among grazing treatments, although a general decrease in its density occurred. However, some significant difference may be noted. The basal coverage of big bluestem in ordinary upland showed a somewhat significantly greater decrease in the lightly stocked pasture than in the moderately stocked or the deferred-rotation pastures. In the limestone breaks site basal coverage of big bluestem decreased significantly more in the moderately stocked pasture than in the deferred-rotation group. In the clay upland site big bluestem decreased significantly less under light stocking than under any other treatment. Both the limestone breaks and clay upland range sites occupy only small areas in the pasture stocked moderately, mostly near the watering place, and tend, therefore, to be somewhat overutilized. Although the number of transect samples obtained from these two limited sites was deemed insufficient for statistical analysis, it was noted that big bluestem decreased on them.

Expressing the abundance of a species as a percentage of the population gives a measure of its relative importance in that population. In the ordinary upland range site only the overstocked pasture has shown a pronounced decrease in percentage of big bluestem. In the limestone breaks range site decreases occurred only in the season-long, moderately and lightly stocked pastures, the others remaining relatively stable throughout the six-year period. In the clay upland range site big bluestem increased at first, then decreased sharply in all pastures. The percentages fluctuated somewhat in the very shallow range site but generally were lowest in 1955.

Little Bluestem. This mid grass is the most abundant dominant in the true prairie. The average basal coverage of little bluestem by pasture, range site, and year is given in Table 2 together with the results of analyses of variance and regression coefficients.

Little bluestem has tended to decline more sharply than the other decreasers under the combined effects of heavy utilization and drought. This species is not so deep rooted as the tall grass decreasers and thus is affected more readily by severe droughts. It gives the appearance of not being grazed closely after early summer, but cattle actually pull the outer leaves from the bunches and thus use it rather closely. Where it is moderately or closely grazed it will remain palatable throughout the grazing season and will continue to be regularly utilized. When this happens increasers and invaders exert greater and greater competitive pressure. The fact that differences were significant in 10 of the 18 analyses of variance given in Table

TABLE 2. Little bluestem; average basal area in number of sq cm per 10-m line transect by range sites and pastures for the years 1950-1955. Results of statistical analyses are given where applicable.

Range site	Pasture No.	YEARS						Regression coefficient
		1950	1951	1952	1953	1954	1955	
Ordinary upland	1 (a)	83.0	47.2	37.7	48.6	39.8	28.8	-6.39
	2	59.8	38.4	28.3	33.3	18.6	19.5	-6.88
	3	56.8	46.5	43.5	65.1	42.4	32.5	-3.14
	4	80.1	58.7	37.9	65.5	44.2	36.4	-6.21
	5	68.6	52.8	38.0	55.5	45.6	39.6	-3.40
	6	97.3	50.5	51.5	68.6	55.0	33.2	-6.43
R (c)								-5.23
Anova results		ns	ns	**	**	**	*	
Limestone breaks	1	42.0	53.0	39.0	39.5	20.5	11.8	-8.98
	2	44.1	25.0	28.6	26.5	30.5	22.3	-1.88
	3	84.9	39.7	48.4	76.9	61.2	38.0	-3.45
	4	97.0	45.3	62.1	67.8	53.5	48.9	-2.34
	5	65.4	62.4	41.9	74.0	64.9	41.8	-0.82
	6	75.1	43.1	50.4	53.8	49.0	40.5	-3.19
R								-2.17
Anova results		ns	**	**	**	**	**	
Clay upland	1	44.5	32.0	33.0	38.0	14.6	4.9	-6.86
	2	38.0	27.1	27.9	24.2	16.5	18.6	-3.14
	3	44.8	40.2	28.6	41.3	26.3	19.0	-4.96
	4	67.9	38.4	25.2	34.7	30.8	10.9	-6.79
	5	48.3	35.5	37.2	41.8	32.5	17.9	-4.09
	6	51.8	37.2	38.0	52.1	26.9	26.7	-3.77
R								-4.98
Anova results		ns	ns	ns	ns	ns	**	
Very shallow (d)	1	31.3	9.7	20.2	19.7	
	2	3.0	11.1	10.2	18.8	4.3	1.4	
	3	64.2	30.9	24.9	28.8	12.0	18.6	
	4	39.0	21.7	20.5	11.8	8.2	
	5	62.0	35.0	52.0	50.0	16.0	21.3	
	6	16.0	5.0	10.4	11.3	
Claypan (e)	4	17.2	19.6	14.1	11.5	13.3	5.5	
	5	9.7	8.0	12.0	1.0	

(a) Pasture 1 moderately stocked, pasture 2 heavily stocked, pasture 3 lightly stocked, and pastures 4, 5, and 6 grazed in a deferred-rotation system.

(b) Results of the analysis of variance for each year by major range site, ns indicating non-significance at the 5% level, * indicating significance at the 5% level, and ** indicating significance at the 1% level.

(c) The weighted mean of the regression coefficient for pastures 4, 5, and 6.

(d) This site occurs in only small areas, thus not enough samples were available for statistical analysis.

(e) This site occurs only in two pastures.

2 suggests that little bluestem fluctuates widely in response to the different grazing treatments. There was significantly less little bluestem on ordinary upland in the overstocked pasture than in the others by 1952, and by 1955 it had also fallen off in the other two season-long pastures. It will be noted that the overstocked pasture had approximately the same amount of little bluestem in 1955 as in 1954, but that substantial reductions occurred in the other pastures from 1954 to 1955.

In the limestone breaks site the overstocked and moderately stocked pastures had significantly less little bluestem than the others during the early years of the experiment and by 1954 the differences were highly significant. In clay upland little bluestem declined in all pastures, especially the one stocked at the medium rate, and by 1955 it was significantly lower

in that pasture than in all others except pasture 4 of the deferred group. This species has also declined throughout the very shallow and claypan range sites.

The relative abundance of little bluestem was also considered in terms of percent of total vegetation. In the ordinary upland range site it has declined sharply in the overstocked pasture and less sharply in the one stocked moderately. The understocked pasture showed a slight increase in percent of little bluestem, while the pastures in the deferred-rotation group fluctuated somewhat. In the limestone breaks range site this species showed a marked percentage decline in the moderately stocked pasture, a slight decline in the heavily stocked one, and remained at about the same level in the others. In the clay upland site there has been a decline in the percentage of little bluestem in all but two pastures, and there it has remained fairly constant. It has decreased in both the very shallow and claypan sites in all pastures.

Indiangrass. This is a tall, coarse grass with water requirements and growth habits similar to those of big bluestem. Next to big bluestem, it is the most abundant tall grass in the experimental area and is an important forage species.

Regression coefficients on data from the three major range sites indicate that indiangrass has decreased in density in all pastures. Its behaviour in this respect resembled that of big bluestem, but there was somewhat greater variability within years of sampling, although the differences among pastures did not continue over the years. Indiangrass declined in the very shallow and claypan range sites.

The percentage of indiangrass has declined in the ordinary upland range site on all pastures since 1952, the heavily stocked having the smallest percentage in both 1954 and 1955. In the limestone breaks and clay upland sites there has also been a general decline in all pastures, the lightly stocked one having the smallest percentage in limestone breaks and the moderately stocked one in the clay upland site. In the very shallow site it was highest under moderate stocking.

Other Decreasers. Switchgrass, prairie dropseed, and prairie junegrass make up such a small percent of the cover in these pastures that statistical analyses were not attempted. However, some observations are of interest. In ordinary upland switchgrass showed a slight, general increase in density but it exhibited no definite trends in the other range sites.

Prairie junegrass is a cool-season mid grass of widespread occurrence but is rather small in stature and seldom is sufficiently abundant in true prairie to be highly productive. In ordinary upland it showed a decrease, especially in the overstocked pasture. It decreased in limestone breaks to the extent that by 1955 it was encountered in the transect samples on only two of the six pastures. There also has been a decrease in clay upland, very shallow, and claypan sites.

Prairie dropseed is a warm-season, mid grass characteristic of the drier uplands in true prairie.

In ordinary upland and limestone breaks it showed an increase in 1955 over the 2 preceding years but no trends were observed in the clay upland, very shallow, or claypan range sites.

Total Increasers. Major increasing grass species taken together make up a considerable part of the vegetation. Change either in their actual or relative abundance may be considered evidence of change in range condition. The grass species making up this total in the trial pastures are sideoats grama, Kentucky bluegrass, buffalograss, blue grama, hairy grama, tumblegrass, windmillgrass, purple lovegrass, seribner panicum, sand dropseed, and tall dropseed.

In practically every instance grasses of this group had shown an actual decrease prior to the drought, but they increased more or less steadily after the drought began. A study of regression coefficients revealed a sharp rise in the overstocked pasture in the ordinary upland range site. The increase was significantly greater in this pasture than in any of the other pastures, and since 1953 this pasture has had more increasers in ordinary upland than any of the others, although at the outset it contained about the same quantity. In the limestone breaks site of the overstocked and moderately stocked season-long pastures, increasers showed a slight rise in contrast to the rather pronounced declines recorded in the other pastures. By 1954 these 2 pastures had significantly greater populations of increasers than the other pastures, and by 1955 the overstocked pasture was even farther ahead in increasers. In the clay upland range site total increasers showed a significant increase in the moderately stocked pasture, a slight increase in the deferred-rotation group, and an actual decrease under heavy stocking.

Increasers taken as percent of plant cover are summarized by pasture, years, and range sites in Table 3. The most significant change is their sharp percentage rise in ordinary upland under close grazing. The percentage rise in limestone breaks was less marked, while in clay upland there was a relative decrease under close grazing, due largely to a sharp drop in Kentucky bluegrass during drought. The overstocked pasture had had the highest percentage of increasers in 1953 and 1954. In the very shallow range site all pastures except the one stocked moderately showed relative increases, while in the claypan site the percentage of increasers remained about the same.

Sideoats Grama. This probably is the most important increaser in the trial area and is one of the most important ones in the true prairie as a whole. Analysis of variance on each year's data within the three major range sites revealed significant differences among pastures in ordinary upland and limestone breaks for all six years. Differences in clay upland tended to be non-significant.

Since 1952 in the ordinary upland range site there has been significantly more sideoats grama in the overstocked pasture than in any of the others. In the limestone breaks site this pasture has had signifi-

TABLE 3. Total increasers; percentages in the total plant population for 1950-1955 for all of the range sites.

Range site	Pasture No.	YEARS					
		1950	1951	1952	1953	1954	1955
Ordinary upland	1	17.0	16.4	20.0	18.9	23.5	20.2
	2	25.9	23.4	26.2	33.0	46.7	57.1
	3	31.1	19.5	22.3	19.6	28.9	25.7
	4	21.5	25.7	30.1	23.2	30.1	132.6
	5	26.0	17.6	24.6	29.4	32.8	37.9
	6	26.7	20.4	19.4	15.9	25.0	35.3
Limestone breaks	1	21.3	8.3	19.3	12.4	32.1	121.7
	2	23.9	33.4	21.4	24.4	25.6	37.9
	3	24.8	31.9	17.6	11.0	10.2	12.3
	4	18.0	25.2	8.7	14.1	15.6	18.2
	5	25.1	16.7	11.2	7.0	13.5	16.9
	6	17.8	16.0	10.5	8.0	12.5	13.3
Clay upland	1	30.2	28.7	41.4	34.5	59.3	67.0
	2	54.2	42.6	39.4	48.2	64.1	148.7
	3	58.3	33.5	38.7	37.7	56.8	65.4
	4	41.1	34.1	31.2	30.5	44.8	51.3
	5	41.6	31.4	30.2	40.7	48.6	55.1
	6	49.8	28.0	27.1	23.0	49.9	34.3
Very shallow	1	18.5	34.5	37.5	15.3
	2	77.1	57.6	64.8	43.5	72.7	82.1
	3	47.7	44.2	46.3	43.0	71.9	63.2
	4	...	22.4	42.4	46.5	66.6	54.8
	5	5.7	29.8	14.0	28.4	45.5	51.1
	6	34.0	39.5	39.2	74.5
Claypan	4	68.9	53.1	51.3	41.2	55.6	60.1
	5	...	67.4	60.6	80.2	75.9	67.8

Pasture 1 moderately stocked, pasture 2 heavily stocked, pasture 3 lightly stocked, and pastures 4, 5, and 6 grazed in a deferred-rotation system.

cantly more sideoats grama than the others since 1953, although the moderately stocked pasture also has been high toward the end of the period.

There was little indication of trend in the density of sideoats grama, although some significant differences were noted in limestone breaks and clay upland. In limestone breaks this species decreased significantly under light grazing while under close, season-long grazing it increased significantly. There was a significantly greater increasing trend in clay upland under moderate and light season-long stocking than under deferred-rotation grazing. In the very shallow range site there was a general decline in 1955 in all pastures. In the claypan site the averages were about the same for 1953 through 1955.

The relative abundance of sideoats grama has also been considered. In ordinary upland there was an increasing percentage difference between the overstocked pasture and the others. In limestone breaks the major differences were that in the heavily stocked pasture sideoats grama has shown a marked relative increase while in the lightly stocked pasture it declined sharply. The moderately stocked and heavily stocked pastures had substantially more sideoats grama than the others in both 1954 and 1955. In clay upland the heavily stocked one had a higher percentage in 1955 than any of the other pastures. In the very shallow site there

has been a decline in sideoats grama in all pastures, but in claypan the percentage has remained virtually unchanged. This species may actually behave as a decreaser in these rather difficult, preclimax sites.

Kentucky Bluegrass. This exotic species has become more or less naturalized and, while it actually is an invader, it behaves generally as an increaser except in periods of prolonged drought when it may virtually disappear under close use.

Kentucky bluegrass does not occur in as large amounts on the limestone breaks site, but in both ordinary upland and clay upland it showed a substantial decline in 1955 because of the drought. The regression coefficients indicate that in most pastures the density remained about the same. In ordinary upland Kentucky bluegrass increased significantly more in the overstocked pasture than in the moderately stocked pasture and the pastures in the deferred-rotation group. In limestone breaks it increased significantly more in the overstocked pasture than in the deferred pastures. In clay upland heavy grazing seemed to favor it until the drought caused it to decline sharply. An outstanding feature in the very shallow site was the large increase of this species in the heavily stocked pasture. In the claypan range site there has been a sharp reduction in the amount of Kentucky bluegrass.

In ordinary upland the percentage of Kentucky bluegrass in the total plant population declined in all pastures from 1954 to 1955. In limestone breaks it showed a decided increase only in the pastures stocked moderately and heavily. In clay upland it increased in these pastures up to 1954, but in 1955 it declined sharply in the latter.

Other Increasers. Buffalograss, blue grama, hairy grama, tumblegrass, windmillgrass, purple lovegrass, scribner panicum, sand dropseed, and tall dropseed occurred in such small amounts in most of the pastures and range sites that statistical analyses were not attempted. The short grasses, buffalograss, blue and hairy grama, tumblegrass, and windmillgrass are actually invaders on climax and postclimax sites in this area, and while they are not abundant on these sites, they sometimes become abundant on the preclimax sites, clay upland, very shallow, and claypan.

The stoloniferous shortgrass, buffalograss, spreads readily when taller competitors are reduced by range depletion. It is especially abundant on drier sites. It has shown some increase in ordinary upland, especially in the overstocked pasture. Only small amounts of buffalograss occur in limestone breaks. In the clay upland, very shallow, and claypan range sites this grass has shown a general though variable increase.

Blue grama is a short bunch grass that occurs sparingly in undisturbed true prairie and usually only in the driest situations where mid grasses do not grow abundantly enough to produce a dense shade. In this study it was present in only small amounts in ordinary upland and limestone breaks, but was relatively more abundant in the preclimax sites.

Hairy grama, a short grass, usually is abundant only on thin droughty soils and rocky outcrops. It has increased in this trial on ordinary upland and limestone breaks sites, but no definite trend has been established in clay upland.

Tumblegrass and windmillgrass are sparingly distributed in the prairie. There was an increase of windmillgrass in the overstocked pasture in the limestone breaks and very shallow sites but no trends were detected in the other sites and pastures.

Purple lovegrass also is sparsely distributed and did not show trends in the small amounts present. Scribner panicum is a low growing, rosette forming perennial that grows between the tufts and bunches of other grasses. Only small amounts of this grass were present in all the sites and trends were not observed.

Sand dropseed is a mid grass that increases readily under droughty conditions. In ordinary upland it increased in the overstocked pasture. In clay upland there was a substantial increase in the moderately and lightly stocked pastures in 1955, while in the very shallow site there was an increase in the lightly stocked pasture in 1955.

Tall dropseed is a drought resistant perennial bunch grass that normally forms only a small part of the vegetation. There was some fluctuation in the amounts present in the experimental area but no trends have developed.

Total Perennial Grasses. Perennial grasses, which constitute the bulk of the plant cover in true prairie, have decreased in abundance on all range sites during the dry years since 1951.

In the ordinary upland site perennial grasses decreased significantly less in the overstocked pasture than in the others and in limestone breaks significantly less in this pasture than in all except the moderately stocked one. In the clay upland site they decreased significantly more in the deferred-rotation pastures than in pastures stocked moderately and lightly. Although some significant differences were found in the three major range sites within years, no one pasture or group of pastures was consistently different from any of the others.

The relative amount of perennial grass in the total plant cover is of some importance. In the ordinary upland and limestone breaks sites all pastures except the overstocked one showed a decline in the percentage of perennial grasses in 1955, and in clay upland all pastures declined in percentage of perennial grasses in the drought year of 1955, the lightly stocked pasture showing the smallest decline. In the very shallow and claypan range sites there has been considerable fluctuation but no very definite trends.

Sedges and Rushes. These are cool season species, resuming spring growth several weeks ahead of the bluestem. Sedges (*Carex* spp.), rush (*Juncus interior*), and spikeweed (*Eleocharis tenuis*) have been grouped together in this study.

The sedges and rushes have shown considerable stability regardless of treatment in all pastures, the only clear cut difference occurring in limestone breaks

where the moderately stocked pasture had significantly more sedges and rushes than any other pasture in 1953 and 1955. There have been percentage declines in both ordinary upland and limestone breaks in 1955. In the very shallow site the moderately stocked pasture showed an increase and deferred grazing a decrease. In claypan, the sedges and rushes have decreased somewhat in pasture 4 of the deferred group.

Annual Grasses. All annuals are invaders in true prairie, their presence in any considerable amount being evidence of decline in range conditions. Of the 14 annual grasses occurring on the experimental area, those most frequently encountered in the sampling were little barley, sixweeks fescue, and annual brome. None of the treatments has as yet caused the invasion of any substantial amounts of annual grasses.

Perennial Forbs. Certain perennial forbs are naturally present in true prairie. Some are relished by stock and decrease under grazing, others increase, and still others stand ready to invade if depletion should occur. The major forbs detected in the sampling thus far are western ragweed, prairie catspaw (*Antennaria campestris*), sagewort (*Artemisia ludoviciana*), heath aster (*Aster ericoides*), goldenrod (*Solidago* spp.), wooly verain, and baldwin ironweed. Smaller amounts of some 80 other perennial forbs were also found.

Differences in numbers of perennial forbs among pastures generally were not statistically significant and did not appear to display any consistent change that might be interpreted as trends. A striking difference in aspect was noted in the over-grazed pasture in the later years of the trial. Baldwin ironweed and buckbrush (*Symphoricarpos orbiculatus*) were much in evidence in this pasture on the limestone breaks and ordinary upland range sites. This difference is illustrated in Fig. 3.



FIG. 3. Contrast in nature of the cover on pasture 2 (heavy stocking) on the right and pasture 3 (light stocking) on the left. Photo taken in mid July, 1954, the sixth year of treatment.

The percentage of perennial forbs for 1950 through 1955 for the 5 range sites was also observed. In ordinary upland this percentage remained about the

same in the moderately stocked pasture while showing an increase in the others. This percentage increase is due to actual reductions in number of grass plants. Similar trends occurred in limestone breaks, but no striking changes occurred in the other sites.

Annual and Biennial Forbs. All of the plants included in this group are invading weeds in the prairie. Some of the most prominent in the experimental area are wavyleaf thistle, curlycup gumweed, croton (*Croton monanthogynus*), Carolina draba (*Draba reptans*), daisy fleabane (*Erigeron ramosus*), snow-on-the-mountain euphorbia (*Euphorbia marginata*), rough falsepennyroyal (*Hedeoma hispida*), wooly plantain (*Plantago purshii*), and johnnyjumpup (*Viola rafinesquii*). Many others are present in smaller quantities, but taken as a group they have not occurred in significant amounts in the trial area.

Woody Plants. Small amounts of shrubs and half-shrubs are present naturally in unmowed prairie. Some, like inland ceanothus (*Ceanothus ovatus*) and leadplant amorphia (*Amorpha canescens*), are useful browse plants. Others are weedy in habit and may increase sharply under abusive grazing. The woody plants detected by the sampling include leadplant amorphia, inland ceanothus, nipple cactus (*Mamillaria* sp.), smooth sumac (*Rhus glabra*), prairie rose (*Rosa suffulta*), and buckbrush. A few other woody species are found primarily in the draws. There did not appear to be any striking differences among pastures or years in the small amounts present.

Total Plant Cover. Density of plants fluctuates with changes in precipitation as it expresses variation in amount of growth resulting from variations in moisture supply. There also may be a tendency toward denser cover under the same weather conditions when plant composition shifts under grazing pressure from tall dominants to short, spreading grasses.

Overstocking caused a smaller decrease in total plant density in the major range sites than did the lighter stocking treatments (Table 4). A study of the regression coefficients shown in Table 4 indicates that in ordinary upland the total plant cover decreased significantly more in pastures stocked moderately and lightly than in the one stocked heavily. In limestone breaks the latter declined significantly less in plant density than all of the other pastures. In clay upland the pastures in the deferred-rotation system showed a significant decreasing trend in plant cover. There was, however, a change in species composition from the tall climax grasses to the short spreading species in the overstocked pastures. There was no definite pattern in the differences among pastures within years. In both the very shallow and claypan range sites there has been some yearly fluctuation, but no trend.

CLIPPING DATA

Forage production on native range may vary widely under natural conditions even in climax. Clippings were taken on the three major range sites in 1953, 1954, and 1955. In 1953 limestone breaks and

TABLE 4. Total plant population; average basal area in number of sq cm per 10-m line transect by range sites and pastures for the years 1950-1955. Results of statistical analyses are given where applicable.

Range site	Pasture No.	YEARS						Regression coefficient
		1950	1951	1952	1953	1954	1955	
Ordinary upland	1 (a)	cm	cm	cm	cm	cm	cm	-14.23
	2	212.8	147.8	139.5	147.7	136.0	99.2	-3.93
	3	201.0	148.6	151.0	149.6	153.2	161.4	-13.91
	4	217.7	153.9	158.8	161.8	145.0	105.5	-9.94
	5	213.9	170.6	151.7	176.6	162.1	135.8	-6.56
	6	213.2	144.3	163.3	156.2	157.8	136.1	-11.76
Anova results	R	235.1	163.5	163.4	155.2	150.5	138.2	-9.25
	(b)	ns	*	ns	ns	*	**	
Limestone breaks	1	183.0	152.4	115.0	115.0	118.0	102.5	-12.27
	2	168.3	132.8	131.0	119.4	134.6	117.7	-2.59
	3	216.3	145.7	159.0	182.2	142.1	94.1	-15.77
	4	220.0	141.2	152.0	155.4	134.7	120.2	-9.33
	5	202.5	153.3	116.3	142.6	144.5	109.8	-10.84
	6	187.7	135.2	151.2	138.3	133.7	103.4	-11.22
Anova results	R							-10.68
	(b)	ns	ns	**	*	ns	ns	
Clay upland	1	182.0	144.9	154.5	180.3	172.5	154.0	1.22
	2	256.5	155.3	166.1	168.4	184.5	139.5	-5.56
	3	258.3	161.1	162.7	170.6	175.5	182.0	-4.14
	4	231.7	159.1	130.3	160.3	165.5	148.9	-5.48
	5	212.0	157.4	165.4	161.7	179.6	143.0	-4.70
	6	240.4	163.0	162.7	156.2	154.0	127.6	-14.16
Anova results	R							-8.09
	(b)	**	ns	ns	ns	ns	ns	
Very shallow (d)	1	93.0	79.3	95.4	87.0		
	2	227.0	141.6	129.6	119.1	142.9	161.0	
	3	256.1	136.5	106.7	148.7	155.1	165.1	
	4	107.0	162.7	106.4	134.0	142.4	
	5	140.0	131.8	129.0	148.0	130.2	154.0	
	6	116.0	89.0	98.0	172.3		
Claypan (e)	4	230.0	165.1	166.3	191.1	182.9	198.4	
	5	128.0	213.0	328.0	187.8	145.0	

(a) Pasture 1 moderately stocked, pasture 2 heavily stocked, pasture 3 lightly stocked, and pastures 4, 5, and 6 grazed in a deferred-rotation system.

(b) Results of the analysis of variance for each year and major range site, ns indicating non-significance at the 5% level, * indicating significance at the 5% level, and ** indicating significance at the 1% level.

(c) The weighted mean of the regression coefficient for pastures 4, 5, and 6.

(d) This site occurs in only small areas, thus not enough samples are available for statistical analysis.

(e) This site occurs in only two pastures.

ordinary upland were not treated separately but were sampled as one unit. In 1953 both total amount of the top growth and mulch were sampled. After studying the samples taken in 1953 it was felt that the amounts of forbs not grazed might bias the utilization estimates, so the relatively unpalatable forbs were thereafter separated from the forage. Thus in 1954 and 1955 each sample was taken in three parts, forage, weeds, and mulch. At the beginning of the 1955 grazing season cages were placed at randomized locations on the three major sites in each pasture so that utilization estimates could be corrected for differences, if any, in quantity of forage produced.

1953 Data. Clippings in 1953 emphasized the close use observed in the overstocked pasture and in the pasture deferred that year.

Differences in mulch were not clear cut, but in

ordinary upland and limestone breaks the pastures grazed season long had only a little more than 70% as much mulch as the pastures in the deferred-rotation group. In clay upland differences were less pronounced.

1954 Data. Again the overstocked pasture and the deferred one had the smallest forage residues in both ordinary upland and limestone breaks (Table 5),

TABLE 5. The average amounts of forage, weeds, and mulch in lbs per acre remaining at the close of the 1954 grazing season. Significant differences are shown where applicable. The means are based on an unequal number of samples.

Past.	Ordinary upland	Past.	Limestone breaks	Past.	Clay upland
	lbs per acre		lbs per acre		lbs per acre
Forage					
2	1089	2	655	2	454
5	1338 *	1	780	1	571
4	1728	5	1475*	3	798
6	1878	4	1806*	4	1305*
1	1964	3	1876	5	1396
3	2145	6	2105	6	1667
Weeds					
4	90	5	119	4	117
5	150	3	152	3	139
1	209	6	161	2	163
2	227 ns	4	183 ns	5	181 ns
6	227	2	225	1	205
3	243	1	284	6	209
Mulch					
2	930	2	597	2	520
4	1199	1	820	3	1058 *
1	1754*	3	1854*	1	1254 *
6	2200	4	2101	4	1287
5	2403	6	2379	6	1391
3	2443	5	2568	5	1515

ns indicates non-significance at the 5% level and * indicates significance at the 5% level.

Pasture 1 moderately stocked, pasture 2 heavily stocked, pasture 3 lightly stocked, and pastures 4, 5, and 6 grazed in a deferred-rotation system.

indicating close removal by livestock. In clay upland, the pastures in the deferred-rotation group had significantly greater amounts of forage cover at the close of the season than those grazed season long, but there were no significant differences in the amount of weeds. The heavily stocked pasture, as was expected, had the smallest quantity of mulch in the three sites sampled, but on the pasture deferred in 1954 the quantity of mulch was low in ordinary upland and in the moderately stocked pasture it was low in limestone breaks.

1955 Data. Wire cages, each covering an area of 4 by 4 ft., were placed at randomized locations on the 3 major range sites in each of the 6 pastures at the beginning of the 1955 grazing season. This made it possible to obtain estimates of differences in production resulting from previous treatment and thereby to correct the 1955 clipping samples of grazed areas. Thus a more accurate estimate of utilization was obtained from the yields taken at the close of the grazing season (Table 6).

The total quantity of forage produced during the growing season in 1955 was substantially smaller in closely grazed areas as the result of a reduction in the

TABLE 6. Forage production in lbs per acre for the 1955 growing season on the 3 major range sites for all 6 pastures. Significant differences are shown where applicable. The means are based on an unequal number of samples.

Past.	Ordinary uplands	Past.	Limestone breaks	Past.	Clay uplands
	lbs		lbs		lbs
2	1318	1	1499	2	505
1	1749*	2	1528	3	968*
5	1836	3	1916*	1	1116
6	1887	5	1947	4	1259
3	2080	4	1958	5	1358
4	2132	6	2083	6	1422
Av.	1834	Av.	1822	Av.	1105

* Indicates significance at the 5% level.

Pasture 1 moderately stocked, pasture 2 heavily stocked, pasture 3 lightly stocked, and pastures 4, 5, and 6 grazed in a deferred-rotation system.

vigor of overgrazed plants. This was reported by Weaver (1950) to result also in a reduction in root growth, forcing plants to be more reliant on surface moisture. In comparisons of the average production per range site, it was found that ordinary upland and limestone breaks produced over 50% more forage than clay upland.

Estimates of the average amounts of forage removed during the grazing season were obtained by correcting the differences between grazed and ungrazed (caged) samples by analyses of covariance for the significant differences found in the ungrazed samples (Table 7). These analyses related grazing use to stocking and to site.

TABLE 7. Average amount of forage removed in lbs per acre for the 6 pastures and the 3 major range sites in 1955. Significant differences are shown where applicable. Means are based on an unequal number of samples.

Past.	Forage removed on the 3 major range sites	Site	Forage removed on the 6 pastures
	lbs		lbs
3	390	Limestone breaks Ordinary upland Clay upland	459
6	503		741*
4	712 *		816
1	752		
2	833		
5	842		

* Indicates significance at the 5% level.

Pasture 1 moderately stocked, pasture 2 heavily stocked, pasture 3 lightly stocked, and pastures 4, 5, and 6 grazed in a deferred-rotation system.

The limestone breaks range site showed significantly lighter utilization than the other two major range sites (Table 8).

Comparisons of beef production⁵ and clipping yields were then made on 1955 data (Table 8). When the estimates of forage removal are compared with the beef production per acre it may be observed that there is a close relationship and that beef production

⁵ Beef gain data were supplied by Professor Ed. F. Smith, Department of Animal Husbandry, Kansas State College.

TABLE 8. The average beef production in lbs per acre for the 1955 grazing season for the 4 grazing treatments.

Pasture	Beef production per acre (lbs)
3	33.8
R	42.5
1	54.0
2	63.4

Pasture 1 moderately stocked, pasture 2 heavily stocked, pasture 3 lightly stocked, and R is the average of the pastures in the deferred-rotation system.

and forage removal fall in the same order. The average amount of forage removed on the deferred-rotation pastures was 686 lbs per acre over the 3 major range sites.

The percentage utilization for 1955 (Table 9) was calculated as follows:

$$\frac{\text{forage under the cages—forage outside the cages}}{\text{forage under the cages}}$$

TABLE 9. Utilization percentage for the 1955 grazing season by pasture and range site.

Pasture	Ordinary upland	Limestone breaks	Clay upland	Ave
	%	%	%	%
1	44	30	82	52
2	60	45	69	58
3	30	3	53	29
4	54	25	56	45
5	60	44	49	51
6	34	34	30	33
R	49	34	45	43

Pasture 1 moderately stocked, pasture 2 heavily stocked, pasture 3 lightly stocked, and pastures 4, 5, and 6 (R) grazed in a deferred-rotation system.

The percentage utilization on the pastures in the deferred-rotation group in 1955 was lower than that on the moderately stocked, season-long pasture, despite the fact that they have been stocked at the same average rate (Table 9). The lightly stocked pasture had an average utilization only half as great as that of the heavily stocked pasture. This is in agreement with the acreage allowances per animal unit. In all of the pastures grazed season-long the utilization is greater on clay upland than on ordinary upland. Limestone breaks tend generally to show the lightest utilization.

Pasture 6 of the deferred-rotation group had a significantly greater yield of unpalatable forbs than any of the other pastures as indicated by samples from the cages. The reason for this is not clear, but the 1955 line transect data had already shown that this pasture had a larger number of perennial forbs.

Pasture 5, also of the deferred-rotation group, actually had a lower yield of weeds in the sample areas protected by cages than in the grazed areas outside the cages, indicating little or no use of weeds under this degree of use. The heavily stocked pasture showed the largest amount of weed removal.

There was no significant difference in the utilization of weeds among the three major range sites.

An important factor in preventing excessive water loss by runoff and evaporation from prairie soil is the protective cover of mulch. Mulch cover has been greatly reduced by close use (Table 10), the heavily stocked pasture exhibiting considerable depletion of the mulch cover. Clay upland had significantly less mulch than the other two major range sites over all six pastures. This site is less productive and more closely utilized than the others, and both factors contribute to the smaller quantity of mulch found there.

TABLE 10. Mulch; the average in lbs per acre found at the close of the 1955 growing season on the 3 major range sites for all 6 pastures. Significant differences are shown where applicable. The means are based on an unequal number of samples.

Past.	Mulch	Range site	Mulch
	lbs		lbs
2.....	734	Clay upland	1091
4.....	1252*	Limestone breaks	1550*
1.....	1435	Ordinary upland	1693
6.....	1612		
5.....	1744		
3.....	1900		

* Indicates significance at the 5% level.

Pasture 1 moderately stocked, pasture 2 heavily stocked, pasture 3 lightly stocked, and pastures 4, 5, and 6 grazed in a deferred-rotation system.

CONCLUSIONS

The goal of range research is to obtain information or to develop techniques that will make it possible to produce maximum, sustained range livestock yields consistent with the maintenance of the forage resource. This study has been concerned with the effects of four grazing treatments on botanical composition, plant density, and herbage and residue yields of true prairie range. Species composition is the most useful criterion by which to estimate range condition and, over a period of years, to detect trend in range condition. Plant density is closely related to weather cycles and other factors which affect the microclimate. Herbage yield comparisons are important in obtaining relative utilization estimates.

Two major factors have influenced the changes in species composition observed in these trials, (1) the grazing treatments and (2) the changing weather cycle from abundant moisture prior to mid 1951 to drought conditions that prevailed since that time. The effect of drought and grazing pressure may not always be easily distinguished, but trends under light stocking and deferred-rotation grazing have furnished some evidence of the influence of drought alone, while trends in the moderately and heavily stocked pastures have shown how drought accentuates the harmful effects of close grazing.

There was an abnormal amount of precipitation in 1951, particularly in May, June, and July, and this had been preceded by 4 yrs of approximately average precipitation. Unusually dry periods occurred in

1952 and 1953, particularly in June and July, and there was a moisture deficit of approximately 6.5 in. in 1954. In 1955 there was not enough early season moisture to compensate for the previous years of drought.

The concept of "climax for the site" deals with the equilibrium of plant composition for any given range site as determined by the combined physical factors of the environment. This equilibrium is considered to represent the potential maximum that the combination of environmental factors will support and, therefore, climax for a range site is not necessarily the climatic climax of the region. However, certain range sites such as ordinary uplands do support the regional climax. An earlier study of the experimental area by Anderson & Fly (1955) revealed six distinct vegetation-soil units termed range sites. In the present study sufficiently large areas of only 3 range sites, ordinary upland, limestone breaks, and clay upland, occurred in all pastures to permit adequate sampling for statistical analyses. However, a few samples were also taken in most years in the very shallow and claypan range sites in the pastures where these sites occurred. Thus it was possible to make some observation on these range sites. The sixth site, lowland, was not sampled because of the great amount of variation due to its gullied condition.

Since the grazing treatments had been started in 1949, line transect data for 1950 through 1955 were used to study the effects of the grazing treatments on botanical composition. The 1947 data were also analyzed to study the degree of homogeneity prior to differential grazing.

The overstocked pastures showed a steady decline in percent of total decreasers in all sites except clay upland where, as a result of the sharp decline in Kentucky bluegrass under drought stress, there actually occurred a slight increase in the percentage of decreasing species of grass in 1955. In the limestone breaks and clay upland range sites there was a great decline of decreasers in the moderately stocked pasture because of the overgrazing of these two sites. Although there was a pronounced decreasing trend in the density of decreasers in all pastures, there were only small changes in the percent of plant population except under heavy grazing use. Little bluestem, a mid grass decreaser, has declined more sharply than the other decreasers under the combined effects of heavy utilization and drought. The percentage of big bluestem has not declined in most pastures, while indiangrass showed a decreasing trend because of the drought.

In contrast to that of the decreasers, both the density and the percentage of increasing species showed a marked increase under close grazing, with the exception that a decrease occurred in 1955 in the heavily stocked pasture. There also was a large increase in the lightly stocked pasture in the clay upland range site because cattle tended to congregate on about two-thirds of this site and graze it rather closely.

The species responsible for the greater part of the change in total increasers have been sideoats grama, buffalograss, and blue grama. Sideoats grama, a mid grass that is tolerant to both overgrazing and drought, showed a marked increase due to overgrazing in both the ordinary upland and limestone breaks range sites. Buffalograss showed a substantial increase on overgrazed ordinary upland. On clay upland there was an increase of both buffalograss and blue grama in pastures moderately and lightly stocked but a decline in the heavily stocked pasture. This would seem on the surface to indicate that the increasing species of grasses have reached a point in deterioration under close use where they too have started to decrease and now are being replaced by invaders. In this case, however, much of the loss of increasers in clay upland were due to the killing of Kentucky bluegrass under close grazing. This ruderal has become more or less naturalized and behaves as an increaser in periods of favorable moisture, but its lack of drought resistance causes it to die out during drought, especially under close use, and thus gives it the appearance of a decreaser. This decline in a species which normally is treated as an increaser, has resulted in a percentage or relative increase of true decreasers when there was no actual increase in their basal cover.

Weaver & Albertson (1939) reported that in the great drought of the 1930's little bluestem, Kentucky bluegrass, and indiangrass were the first species to be affected. The same trends have been observed in these trials. However, they have not yet become so pronounced as those reported by Weaver and Albertson even though the deficit in precipitation has been about as great in the present drought. Higher temperatures accompanied the drought of the 1930's while the drought of the mid 1950's, on the other hand, was preceded by a period of abnormally heavy precipitation.

The percentage of climax or original vegetation is the sum of all decreasers present plus the amounts of increasers normally present in the climax. This value is a quantitative expression of range condition (Dyksterhuis 1949). Table 11 gives an estimate of range condition based only on the perennial grasses for 1950 and 1955 for the 6 pastures on the three major range sites. These figures are quite conservative, therefore, since forbs and sedges were not included.

Heavy grazing has caused a marked reduction in the percentage of climax grasses in ordinary upland. There also has been a reduction, although less marked, under moderate grazing and deferred-rotation grazing. The drought appears to be responsible for this later effect since even moderate stocking under normal conditions is likely to behave as overstocking in dry years. The climax vegetation remained virtually unchanged under light stocking on ordinary upland. There has been a decline in range condition in limestone breaks in pastures stocked both heavily and moderately, while the pastures in the deferred-rotation group have remained virtually unchanged and the

TABLE 11. Range condition percentage based on the percentage of perennial grasses in the climax vegetation for 1950 and 1955.

Site	Pasture	1950	1955
Ordinary upland	1	75	63
	2	67	36
	3	69	59
	4	74	53
	5	68	51
	6	68	52
Limestone breaks	1	73	53
	2	69	52
	3	64	75
	4	76	71
	5	75	76
	6	79	73
Clay upland	1	69	40
	2	55	54
	3	62	50
	4	77	50
	5	68	71
	6	60	62

Pasture 1 moderately stocked, pasture 2 heavily stocked, pasture 3 lightly stocked, and pastures 4, 5, and 6 grazed at an average stocking rate equivalent to that of moderate stocking but in a deferred-rotation system.

lightly stocked pasture has shown an improvement in range condition.

That density is not a good indicator of range condition is indicated by the great relative decrease of total cover in the pastures with the highest range conditions. This is due to the fact that the mid and tall grass dominants have a smaller basal coverage than the less productive short grass increasers. Clippings made at the close of the 1953, 1954, and 1955 growing seasons gave added evidence that heavy stocking is detrimental. The sampling in 1953 and 1954 was on grazed areas only and showed that the utilization was high in the major range sites under heavy stocking and in limestone breaks and clay upland in the pasture stocked moderately. Placing cages in the 3 major range sites on all 6 pastures at the beginning of the 1955 grazing season made it possible to obtain estimates of total ungrazed forage production for the year.

Clipping data in 1955 revealed that over all the pastures, limestone breaks showed only 62% as great a degree of utilization as ordinary upland. This may be taken to indicate that in pastures having steep slopes along with gently rolling uplands the proper degree of use for the steep slopes would be only about 30 to 35% rather than the customary 50%. Heavier utilization than this on the steep slopes would lead to overutilization of the less steep parts of a range pasture. It also is quite likely that the extra residue accumulated under light use is required on the steeper slopes to control runoff and soil loss.

Another important finding was that the clay upland range site produced only 60% as much forage as the ordinary upland and limestone breaks sites in 1955. Therefore, in estimating safe stocking rates for this preclimax site it may be appropriate to use

grazing values from the rainfall belt of 10 in. below the average for climax sites instead of 5 in. below as suggested by Dyksterhuis (1949) and outlined in the Soil Conservation Service Technicians Guides for the Flint Hills.

Utilization of weeds in 1955 was greater in the overstocked pasture than in the others despite the fact that this pasture included a greater amount of the less palatable increasing and invading species. Cattle on this pasture apparently were forced to graze those less palatable ones because of a reduction in amount of readily available forage.

Underutilization, as in the lightly stocked pasture, resulted in a significantly larger accumulation of mulch than did moderate use. Experiments by Weaver & Fitzpatrick (1934) showed that heavy accumulations of debris may greatly retard growth in spring. This retardation of plant growth in early spring is considered by Flint Hills ranchers to be a hindrance in grazing management where rapid early season gains are desired. Weaver & Rowland (1952) reported that a dense mulch also resulted in sparser stands of the dominants and lower yields from them. In these trials the plant density has been greatly reduced under light stocking but forage yields have remained unaffected.

Continuous overutilization of forage resulted in a significantly smaller amount of mulch. Reduction in amount of soil-protecting mulches leads to increased water losses by runoff and perhaps also to increased surface evaporation. Excessive moisture losses contribute to reductions in plant vigor and the subsequent establishment of the less productive, drought resisting species. Thus droughtier soil conditions can be brought about by overgrazing alone. This appears to have occurred in the overstocked pasture. A continuation of overgrazing will result in still droughtier conditions with an increase in unpalatable weeds and short-lived annual plants which can take advantage of the rainfall shortly after it occurs. Meanwhile the vegetation and mulch become more sparse until there is more and more bare ground. This may allow severe erosion. At any point in this chain of events, a subere may be initiated simply by reducing the grazing pressure. Thus under proper stocking and with average precipitation climax vegetation may be eventually restored, the length of time required depending upon the degree of depletion and the seral stage.

SUMMARY

An experimental area was set aside in 1949 to evaluate the response of true prairie vegetation on major Flint Hills range sites to grazing treatment. The grazing treatments compared were heavy, moderate, and light season-long stocking and deferred-rotation stocking at the moderate rate. The results are reported in terms of vegetational responses by range sites. Major emphasis is on species composition and on trends which develop under the different intensities and methods of utilization. Herbage and mulch yields also were studied.

The major factors influencing the changes in plant composition in the trials were the grazing treatments and the changing weather cycle from abundant moisture prior to mid 1951 to drought conditions that prevailed through 1955. However, major differences may be separated. Heavy stocking caused a steady decline in percent of total decreasing species of grasses in all range sites except clay upland. Little bluestem has declined more sharply than the other decreasers under the combined effects of heavy utilization and drought. In clay upland there was a slight increase in the percentage of decreasers in 1955 due largely to the sharp decline in Kentucky bluegrass. In the limestone breaks and clay upland range sites there was a significant decline of decreasers in the moderately stocked pasture because these sites are located near the source of stock water in this pasture and would be overgrazed even under light stocking. The percentage of increasing species of grasses showed a marked rise under close grazing except in 1955. The species most responsible for the change in increasers are sideoats grama, buffalograss, and blue grama.

Uneven distribution of grazing use has resulted in overgrazing of small areas in both the moderately and lightly stocked pastures.

Six years of overgrazing resulted in a decrease in amount of forage produced due to the reduction in vigor of the range plants and a shift to less productive preclimax species.

Moderate season-long stocking resulted in closer use of the forage than occurred under deferred-rotation stocking at the same average stocking rate.

Proper degree of forage use on the limestone breaks range site was suggested as being 10 to 35% rather than the 50% customary on gentler slopes if overgrazing of the latter is to be avoided.

Clay upland produced only 60% as much forage as ordinary upland and limestone breaks. This must be taken into account when calculating stocking rates for areas including such droughty, preclimax sites.

Plant density has been greatly reduced under light stocking, but the forage yields have remained unaffected. The large amount of mulch that accumulated on understocked ordinary upland and limestone breaks sites has tended to encourage excessive utilization of clay upland where the mid and short grasses prevail and where the mulch accumulation was much smaller.

Continuous overutilization of forage resulted in significantly reduced amounts of mulch. This will permit increased loss of water by runoff.

These results suggest that for sustained maximum forage production, range management based on range condition classification is essential.

LITERATURE CITED

- Ahlgren, H. L. 1947. A comparison of methods used in evaluating the results of pasture research. *Agron. Jour.* 39: 240-259.
- Aldous, A. E. 1938. Management of Kansas bluestem pastures. *Jour. Amer. Soc. Agron.* 30: 244-253.
- Anderson, K. L. 1940. Deferred grazing of bluestem pastures. *Kans. Agr. Expt. Sta. Bull.* 291.

- . 1942. A comparison of line transects and permanent quadrats in evaluating composition and density of pasture vegetation of tall prairie grass type. *Agron. Jour.* 34: 805-822.
- . 1951. The effects of grazing management and site conditions on Flint Hills bluestem pastures in Kansas. Unpublished Ph.D. thesis, University of Nebraska, Lincoln, Nebraska.
- Anderson, K. L. & C. L. Fly. 1955. Vegetation-soil relationships in Flint Hills bluestem pastures. *Jour. Range Mgt.* 8: 163-169.
- Brinegar, T. E. & F. D. Keim. 1942. The relations of vegetative composition and cattle grazing on Nebraska range land. *Nebr. Agr. Expt. Sta. Res. Bull.* 123.
- Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. *Jour. Forestry* 39: 388-394.
- Craddock, G. W. & C. L. Forsling. 1938. The influence of climate and grazing on spring-fall sheep range in southern Idaho. *U. S. Dept. Agr. Tech. Bull.* 600.
- Dyksterhuis, E. J. 1949. Condition and management of range land based on quantitative ecology. *Jour. Range Mgt.* 2: 104-115.
- Fly, C. L. 1946. Natural agricultural resource areas of Kansas. *Soil Conservation in Kansas. Kans. State Bd. Agr. Rpt.* 65: 126-195.
- Hanson, H. C. 1950. Ecology of the grassland. II. *Bot. Rev.* 16: 283-360.
- Hanson, H. C., L. D. Love & M. S. Morris. 1931. Effects of different systems of grazing by cattle upon a western wheat-grass type of range near Fort Collins, Colorado. *Colo. Agr. Expt. Sta. Bull.* 377.
- Herbel, C. H. 1954. The effects of date of burning on native Flint Hills range land. Unpublished M.S. thesis, Kansas State College, Manhattan, Kansas.
- Nelson, E. W. 1934. The influence of precipitation and grazing upon black grama grass range. *U.S. Dept. Agr. Tech. Bull.* 409.
- Nevens, W. B. 1945. A comparison of sampling procedures in making pasture yield determinations. *Jour. Dairy Sci.* 28: 171-185.
- Parker, K. W. & D. A. Savage. 1944. Reliability of the line interception method in measuring vegetation on the Southern Great Plains. *Agron. Jour.* 36: 97-110.
- Sarvis, J. T. 1923. Effects of different systems and intensities of grazing upon the native vegetation at the Northern Great Plains Field Station. *U.S. Dept. Agr. Bull.* 1170.
- Savage, D. A. 1937. Drought survival of native grass species in the central and southern Great Plains, 1935. *U.S. Dept. Agr. Tech. Bull.* 549.
- Smith, C. C. 1940. The effect of overgrazing and erosion upon the biota of the mixed-grass prairie of Oklahoma. *Ecology* 21: 381-397.
- Stoddart, L. A. & A. D. Smith. 1943. *Range Management*. New York: McGraw-Hill Book Co. 547 pp.
- Weaver, J. E. 1950. Effects of different intensities of grazing on depth and quantity of roots of grasses. *Jour. Range Mgt.* 2: 100-113.
- . 1954. *North American Prairie*. Johnsen Publ. Co., Lincoln, Nebr. 348 pp.
- Weaver, J. E. & F. W. Albertson. 1939. Major changes in grassland as a result of continued drought. *Bot. Gaz.* 100: 576-591.
- Weaver, J. E. & R. W. Darland. 1948. Changes in vegetation and production of forage resulting from grazing lowland prairie. *Ecology* 29: 1-29.
- Weaver, J. E. & T. J. Fitzpatrick. 1934. The prairie. *Ecol. Monog.* 4: 109-294.
- Weaver, J. E. & W. W. Hanson. 1941. Native mid-western pastures, their origin, composition, and degeneration. *Nebr. Conserv. & Surv. Div. Bull.* 22: 93 pp.
- Weaver, J. E. & N. W. Rowland. 1952. Effects of excessive natural mulch on development, yield, and structure of native grassland. *Bot. Gaz.* 114: 1-19.
- Weaver, J. E. & G. W. Tomanek. 1951. Ecological studies in a midwestern range: the vegetation and effects of cattle on its composition and distribution. *Univ. Nebr. Cons. & Surv. Div. Bull.* 31.

